

FOSSIL MAMMALS OF AFRICA No. 21  
MIOCENE RHINOCEROSES OF EAST AFRICA



BY

DIRK ALBERT HOOIJER D.Sc.

*Hooijer*

Rijksmuseum van Natuurlijke Historie, Leiden

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## MIOCENE RHINOCEROSES OF EAST AFRICA

By D. A. HOOIJER

A en juger d'après l'assurance avec laquelle certains auteurs ont attribué des noms spécifiques aux restes les plus insignifiants de Rhinocéros fossiles, on pourrait croire que la détermination des animaux de ce groupe est chose aisée. Ceux qui se sont sérieusement occupés de ce sujet savent que le contraire est vrai.

H. G. STEHLIN

### CONTENTS

|   | <i>Page</i> |
|---|-------------|
| I. INTRODUCTION AND ACKNOWLEDGEMENTS . . . . .                                | 119         |
| II. SYSTEMATIC DESCRIPTIONS . . . . .   | 122         |
| <i>Dicerorhinus leakeyi</i> sp. nov. . . . .                                  | 122         |
| <i>Aceratherium acutirostratum</i> (Deraniyagala) . . . . .                   | 136         |
| <i>Brachypotherium heinzlini</i> Hooijer . . . . .                            | 142         |
| <i>Chilotherium</i> sp. . . . .   | 150         |
| POSTCRANIAL SKELETON OF <i>Dicerorhinus</i> AND <i>Aceratherium</i> . . . . . | 152         |
| III. DISTRIBUTION OF RHINOCEROSES OVER EAST AFRICAN MIOCENE SITES . . . . .   | 183         |
| IV. TIME PLACEMENT OF THE MIOCENE EAST AFRICAN FAUNAS . . . . .               | 185         |
| V. REFERENCES . . . . .   | 187         |

### SYNOPSIS

Four species of Rhinocerotidae are described from the Tertiary (Miocene) of East Africa, including a new species *Dicerorhinus leakeyi*. The bearing of these Rhinoceroses on the time placement of the Miocene East African faunas is discussed, resulting in a tentative correlation with the Burdigalian of Europe, although some of the Rusinga sites appear to be younger, later Miocene or even Pliocene.

### I. INTRODUCTION AND ACKNOWLEDGMENTS

RHINOCEROSES have a reputation for being difficult animals to deal with as fossils. In spite of an enormous amount of scientific literature, the present state of our knowledge and comprehension of this group is comparable only to that of O. C. Marsh's grasp of the equids.<sup>1</sup> H. F. Osborn's oft-cited "Phylogeny of the rhinoceroses of Europe" (1900) has never been followed up by a monographic treatise, and the first part of his "The extinct rhinoceroses" (1898), the only part ever published, is devoted to generalities and the acerathere rhinoceroses of the White River Beds of Nebraska and the Dakotas. A comprehensive paper on the Tertiary Rhinocerotidae of Eurasia is sadly lacking and treatment of the fossil material in the scattered literature is very uneven and incomplete.

For a sound diagnosis of a new fossil species we need the whole skull, with the

<sup>1</sup> This sagacious comment was made by Dr. Stanley Westoll in the discussion following my paper at the Symposium of Vertebrate Palaeontology and Comparative Anatomy in Bristol on 23rd September, 1964.

incisors and canines, if any (premaxillaries have often been lost). We need also the skeleton, in particular the metapodials, which are rarely found associated with a skull. These requirements, therefore, are seldom fulfilled (cf. my motto, taken from Stehlin 1925: 106). Too much reliance has often been placed upon individually variable molar crown structures or labile cingula. New fossil species (and genera) have occasionally been based on milk teeth mistaken for permanent teeth, or on female specimens of previously described forms. Fragmentary fossil remains of rhinoceroses have more than once been described as hippopotami, and vice versa. Foot bones have been confounded with those of anthracotheres or chalicotheres. Wrong identifications, once published, have a habit of perpetuating themselves in the literature, to the detriment of a better understanding. In order to soften these pontifical remarks I hasten to add that I have not been able always to avoid these pitfalls in my own rhinoceros work either.

In the last few decades representatives of three genera of Rhinocerotidae from the Tertiary of Eurasia have been found in Africa. These are *Dicerorhinus*, *Aceratherium* and *Brachypotherium*.

The so-called phyletic line of *Dicerorhinus* Gloger comprises a number of evidently collateral forms with slender limbs and feet ranging from the Aquitanian (Upper Oligocene) through the Pleistocene of Europe, and up into the Holocene of Asia. It seems unlikely that the fossils should all be referred to the same genus, and that this is the genus of the extant Sumatran species. *D. sumatrensis* (Fischer) is the most primitive among the five surviving species of rhinoceroses, and may truly be said to represent a Miocene stage of evolution of teeth and skeleton, but its immediate ancestry is unknown apart from what can be derived from subfossil remains found in Sumatran caves (Hooijer 1946a, b). This suggests a decrease in tooth and limb size since the formation of the cave deposits (presumably Early Holocene), which is a common phenomenon. The further use of the generic name *Dicerorhinus* for the Tertiary and Pleistocene forms, however, is to be recommended; we have far too many generic names in the Rhinocerotidae anyway (many monotypical), and it is a relief to see a case in which the generic limits are drawn as broadly as in *Dicerorhinus*. The first African representative to become known is the well-documented *Dicerorhinus primaevus* Arambourg (1959) from the Pontian (Lower Pliocene) of Wad el Hammam in Algeria; earlier records are ambiguous.

The genus *Aceratherium* Kaup, with its persistently tetradactyl fore feet, and limbs as slender as in *Dicerorhinus*, ranges from the Stampian (Middle Oligocene) up into the Pontian in Europe and Asia, showing some phylogenetic advance. It was first recorded from East Africa (Moruaret Hill near Losodok or Lothidok, Kenya) by Deraniyagala (1951) as *Turkanatherium* Deraniyagala; Arambourg's earlier record of a lower molar, an epistropheus, an astragalus, two metatarsals and some phalanges from Losodok as *Aceratherium*? spec. might also belong to *Dicerorhinus*. The dentition of *Aceratherium acutirostratum* (Deraniyagala) has recently been described from the Miocene of the Karugamania region, Lake Albert, Western Rift Valley in Congo (Hooijer 1963).

In the short-limbed and -footed genus *Brachypotherium* Roger of Europe (Burdi-

galian (Lower Miocene) through Pontian), often placed in the North American genus *Teleoceras* Hatcher that may have been derived from it (Osborn 1910 : 292), there is some evolutionary progress (in the shortening of the limbs and metapodials particularly). In 1920 Fourtau recorded this genus (as *Teleoceras*) from the Burdigalian of Moghara in Egypt, and I have added a more progressive species from the Miocene of the Sinda-Mohari region, Lower Semliki, Congo (Hooijer 1963).

Thus, there are various previous records of Tertiary Rhinocerotidae from Africa (in this connexion mention should be made of the well-described but specifically unidentified last upper molar from Karungu, Kenya, recorded by Andrews 1914). Sonia Cole (1950) listed *Aceratherium* from the Miocene of Rusinga Island, Karungu, and Maboko Island, as well as *Teleoceras* from Rusingu and Karungu (Cole 1950 : 29), and also published a photograph of a rhinoceros skeleton in the process of being excavated from the Lower Hiwegi Beds in Rusinga in 1947 (1950, pl. 1). In a provisional list of the Miocene faunas of East Africa, Le Gros Clark & Leakey (1951 : 5) recorded Rhinocerotidae from the following nine sites : Karungu, Rusinga Island, Chianda Uyoma, Ombo, Maboko Island, Songhor, Losodok, Loperot and Tambach.

The collections described in the present paper, upon which the above cited locality records are based, are for the most part in the National Museum Centre for Prehistory and Palaeontology, Nairobi, Kenya, and were generously offered to me for study and report by Dr. L. S. B. Leakey in April, 1963. Much Miocene East African rhinoceros material is in the Department of Palaeontology of the British Museum (Natural History), London, and this I have been lent. Dr. W. W. Bishop of the Kampala Museum, Uganda, has sent me Miocene material from the Napak volcanics, Karamoja, Uganda, which is likewise described in the present paper.

I am very much indebted to Dr. L. S. B. Leakey for entrusting this interesting material to me, as well as to Dr. W. W. Bishop for the Napak material and to Dr. A. J. Sutcliffe for arranging to have the British Museum material made available. I am very grateful to Mrs. S. C. Coryndon, Mrs. Sonia Cole and Dr. T. Whitworth for valuable information and kind advice.

A systematic account of the genera and species of Rhinocerotidae from the East African Miocene is given in the following chapters. The specimens from the British Museum (Natural History) have numbers preceded by an M. The conventional dental nomenclature has been used and the measurements of the cheek teeth have been taken at the base of the crown, the length (ant. post.) in the upper P and M externally except in M<sup>3</sup>, where it is taken internally. Most of the specimens, in addition to the catalogue number, bear letters indicating the sites, such as R. for Rusinga Island, Rs. for a surface find in Rusinga, followed by a sub-site number, e.g., R.1, R.2, etc. (Le Gros Clark & Leakey 1951 : 10) ; K stands for Karungu, KB or MB for Maboko (= Kiboko) Island, and S or Sgr for Songhor (Whitworth 1958 : 2). Maps showing the location of the various sites in Kenya and Uganda will be found in Whitworth (1958 : 2) and Bishop (1958), a map showing the sub-sites in Rusinga was given by Le Gros Clark & Leakey (1951 : 9). On the advice of Dr. Leakey the relationship of the sites to the fossiliferous strata in Rusinga Island has been omitted at this stage.

## II. SYSTEMATIC DESCRIPTIONS

Genus *DICERORHINUS* Gloger 1841*Dicerorhinus leakeyi* sp. nov.

(Pls. 1-3 ; Pl. 4, figs. 1, 4, 7, 8 ; Pl. 5, figs. 1-3 ; Pl. 6, figs. 7, 8, 12 ; Pl. 7, figs. 5, 6 ; Pl. 10, figs. 4, 5 ; Pl. 11 ; Pl. 13, figs. 1-5 ; Pl. 14, fig. 1 ; Pl. 15)

DIAGNOSIS. *Dicerorhinus* species with frontal and nasal horns ; upper incisors smallish, small incisors between lower canines ; inferior squamosal processes united below subaural channel. Occiput as highly elevated as in *D. sansaniensis* (Lartet). Lower border of mandible nearly straight as in *D. sansaniensis*, not curved upward in symphyseal region as in *D. schleiermacheri* (Kaup), *D. orientalis* (Schlosser) and *D. ringstroemi* Arambourg. Size of skull as in *D. schleiermacheri* and *D. orientalis*, larger than in *D. sansaniensis* and smaller than in *D. ringstroemi*. Teeth intermediate in size between those of *D. schleiermacheri* and those of *D. sansaniensis*.

Upper premolars with protoloph and metaloph united internally up to at least 15 mm. from crown base, cingulum weak, protocone not markedly constricted off. Upper molars with low and wide lingual entrance to medisinus, internal cingulum very weak or absent, protocone not or hardly constricted off, antecrochet not prominent, not blocking medisinus, ectoloph depressed between the roots, crochet and crista weak or absent, M<sup>3</sup> bulging out at junction of ectoloph and metaloph.

The specific name is given in honour of Dr. L. S. B. Leakey, who collected the type in 1935.

HOLOTYPE. The skull and associated mandible from Rusinga (Pl. 1 ; Pl. 2, figs. 1, 2).

HORIZON AND LOCALITY. Lower Miocene ; Rusinga Island, Kenya.

DESCRIPTION. The skull and associated mandible were collected at Rusinga by Dr. L. S. B. Leakey in 1935. Both are somewhat crushed and in part restored or fortified with plaster. The crushing is mostly laterally : the two upper tooth-rows are only 30 mm. apart in the premolar region and 50 mm. between the last molars. The tooth-rows are somewhat displaced longitudinally : the right tooth-row is shifted 2 cm. backward relative to the left. The palate is broken. The whole of the post-dental basal portion of the skull is lost except for the right zygomatic arch and glenoid cavity with the postglenoid and post-tympanic processes. The zygomatic arch is pushed inward and slightly backward, reducing the width of the temporal fossa to a mere 3 cm. Of the glenoid cavity the outer portion is displaced backward ; the outer angle of this cavity is on the same transverse level as the huge postglenoid process. This distortion evidently took place while the condyle of the mandible was lodged in the cavity, for the condyle is deformed in the same way, with its outer part pushed backward, and it fits exactly into the cavity as it is. Only a small portion of the left parietal is preserved, and it is thrust upward.

When viewed from the right side, however, the fronto-parietal surface is relatively well preserved, rising backward and upward from the orbit in a gentle curve which

seems unaffected by distortion. The top of the occiput has broken off. The right fronto-parietal crest is preserved, and evidently did not meet its fellow on the other side of the skull, the least distance between the crests being approximately 3 cm. The temporal crest is for the most part preserved, but undamaged only in its lower portion. Below the external auditory meatus the two inferior squamosal processes are seen to be firmly united.

On the ventral surface of the skull nothing remains behind the last molars but the base of the pterygoid process on the left side. The hinder margin of the palate is on a level with the front of  $M^2$ .

The frontal region of the skull is only superficially damaged, and it is clear that there is a median boss just above the anterior border of the orbit, indicating the presence of a frontal horn. The postorbital processes of the frontals are damaged, and the width of the skull at this point cannot be determined. The anterior border of the orbit is above the anterior border of  $M^2$ . The nasal bones are well preserved on both sides, although laterally compressed, and are convex and rugose above, pointing to the presence of a nasal horn. The tips of the nasals are slightly bent downward. The nasomaxillary notch is well shown on either side, extending backward to above the anterior border of the first tooth, the well-worn  $DM^1$ . The depth of the notch is 16 cm. from the nasal tips on the left, and 18 cm. from the tips on the right side. Only 25 mm. behind it there is the infraorbital foramen, placed above  $P^2$ .

The premaxillaries are fortunately preserved in the skull, forming two strong, 4 cm. high, converging bones that are slightly inclined downward. They each carry a relatively small incisor, but no other teeth behind these. The premaxillary-maxillary suture is obliterated, but together with the maxillary processes to which they are attached the premaxillaries have a length of 14 cm., projecting only slightly less forward than the nasals. The height from the lower surface of the tips of the premaxillaries to the tips of the nasals is 11 cm.; the height of the skull from the alveolar margin of  $M^1$  to the upper surface of the frontals is approximately 16 cm.

The mandible belonging to the skull is well preserved on the right side; the left body is broken off behind  $M_2$ . The high ascending portion with the coronoid and condyloid processes fits well into the laterally compressed temporal fossa, and the distorted condyle articulates in the glenoid cavity when the tooth-rows are in occlusion. The lower canines are close to their antagonists, the upper incisors. Between the canines the mandible shows two small incisors. The profile of the mandible is nearly straight ventrally, with the symphyseal portion only slightly curved upward, and the angular process is broad and well rounded behind.

The characters of the present skull and mandible, notably the indications of the presence of a nasal and of a frontal horn, the presence of smallish upper incisors, the small incisors between the lower canines and the union of the two inferior squamosal processes, leave no doubt as to their belonging to the genus *Dicerorhinus*. To this genus a number of Tertiary and Pleistocene species have been referred, evidently forming several collateral lines, in Europe as well as in Asia, where it survives as the Sumatran rhinoceros, *Dicerorhinus sumatrensis* (Fischer). The extant form is not the most advanced: although it lacks the central lower incisors present in the fossil

forms it has an opening between the postglenoid and the post-tympanic process, a supposedly less specialized character than the union of these seen in fossil *Dicerorhinus* (see Flower 1876 : 456).

A second individual of *Dicerorhinus leakeyi* from Rusinga is represented by an upper dentition and right zygomatic arch, and a mandible of which only the right half is entirely preserved. These specimens are marked no. 2, R.1, 1947. The upper dentition agrees perfectly with that of the holotype skull of *D. leakeyi* in characters, and the lower jaw differs only in being slightly convex anteroposteriorly below, longer, less high below  $M_3$ , and in the absence of  $P_1$  (Pl. 2, figs. 3-4).

Measurements of the holotype skull and mandible of *D. leakeyi* as well as of the lower jaw no. 2 from Rusinga are given in Table 1 together with those of *Dicerorhinus sansaniensis* (Lartet) from the Vindobonian of Sansan (Kaup 1854 : 3 ; Filhol 1891 : 200), *Dicerorhinus schleiermacheri* (Kaup) from the Pontian of Eppelsheim (Kaup 1834 : 40-41), *Dicerorhinus orientalis* (Schlosser) from the Pontian of Pikermi (Gaudry 1862-67 : 184, as *Rh. pachygnathus*, and p. 206, as *Rh. schleiermacheri* ; see Ringström 1924 : 12), and *Dicerorhinus ringstroemi* Arambourg (1959 : 73) from the Pontian of North China (Ringström 1924 : 12, as *D. orientalis*). Table 1 shows that the Rusinga form is rather similar in size to *D. schleiermacheri* and *D. orientalis*, *D. sansaniensis* being smaller, and the Chinese species larger.

TABLE I  
Measurements of skull and mandible of *Dicerorhinus* (mm.)

|   | <i>D. leakeyi</i> |       | <i>D. sansaniensis</i> | <i>D. schleiermacheri</i> | <i>D. orientalis</i> | <i>D. ringstroemi</i> |
|---|-------------------|-------|------------------------|---------------------------|----------------------|-----------------------|
|   | Type              | no. 2 |                        |                           |                      |                       |
| Length from occipital crest to tip of nasal bones         | c. 630            | —     | 468                    | 640                       | 645                  | 745                   |
| Width over postorbital processes                          | —                 | —     | —                      | 200                       | —                    | 236                   |
| Height of occiput from basion                             | —                 | —     | —                      | 200                       | 210                  | 220                   |
| Depth of naso-maxillary notch from tip of premaxillaries  | c. 145            | —     | —                      | 142                       | —                    | —                     |
| From naso-maxillary notch to anterior border of orbit     | c. 135            | —     | 95                     | 160                       | 150                  | —                     |
| From anterior border of orbit to external auditory meatus | 260               | —     | 218                    | 246                       | —                    | —                     |
| From tip of premaxillaries to anterior border of $P^2$    | 150               | —     | —                      | 154                       | —                    | —                     |
| Length of mandible from front to back of angular process  | 500               | 530   | 470                    | 510                       | c. 500               | 635                   |
| Length from front to $P_2$                                | 110               | 90    | —                      | —                         | 90                   | c. 95                 |
| Length of symphysis                                       | 130               | 120   | 115                    | 142                       | —                    | 132                   |
| Height below $M_3$  | 105               | 85    | 70                     | —                         | 90                   | 115                   |
| Height of coronoid process                                | c. 275            | 270   | —                      | 278                       | —                    | —                     |
| Height of condyloid process                               | 230               | 220   | 192                    | 248                       | —                    | —                     |

The *Dicerorhinus* skull from Rusinga differs from that of *D. schleiermacheri* as figured by Kaup (1834, pl. 10, fig. 1 ; 1854, pl. 10, fig. 1) in the occiput being more



elevated; the fronto-parietal profile is more concave. There is a marked sagittal crest in *D. schleiermacheri*, and the premaxillaries are not inclined downward as in the Rusinga skull but project straight forward. The symphyseal portion of the mandible is much more curved upward in *D. schleiermacheri* than in *D. leakeyi* so that the upper I and the lower C nearly touch each other just the same. The infraorbital foramen is placed further back in *D. schleiermacheri* than in *D. leakeyi*, viz., c. 40 mm. behind the naso-maxillary notch and above P<sup>3</sup>. The lower border of the mandible is not straight, but slightly concave behind the symphysis in *D. schleiermacheri*; the angular process, however, is equally rounded.

The almost equally large skull of *D. orientalis* from Pikermi (Gaudry 1862-67: pl. 32, fig. 1, as *Rh. schleiermacheri*) likewise has the occiput less elevated than the Rusinga skull, but it does not have a sagittal crest. The premaxillaries are incomplete and carried either reduced incisors or none at all (Ringström 1924: 18-20). The infraorbital foramen is nearer to the naso-maxillary notch (12-18 mm.) and is placed above P<sup>3</sup>. The mandible of *D. orientalis* (Gaudry 1862-67: pl. 28, fig. 1, as *Rh. pachygnathus* but referred to *orientalis* by Ringström 1924: 21) has a slightly convex lower margin; the angular portion is incomplete, but the lower canines are quite reduced.

The skull of *D. ringstroemi* from China (Ringström 1924: 6, text-figs. 1, 2) again does have the flat profile of *D. schleiermacheri* and *D. orientalis*; the fronto-parietal crests do not meet and form no sagittal crest (least distance 45 mm.). The maxillary processes and the premaxillaries have broken off. The mandible (Ringström 1924: 10, text-figs. 3, 4) has a slightly convex lower profile and quite reduced canines, as in *D. orientalis*; the symphysis is curved upward.

It is only in the skull and mandible of *D. sansaniensis* (Duvernoy 1853: pl. 1, fig. 1a; Kaup 1854: pl. 10, fig. 2; Filhol 1891, pls. 13, 14) that the salient characters of *D. leakeyi* are present. The occiput is raised to the same extent as in the Rusinga skull, and the mandible is not much curved upward in its symphyseal portion and nearly straight below in profile. Unfortunately the premaxillaries are missing in the Sansan skull, but the lower C are present. They are relatively well developed and between them there are two small incisors.

Unfortunately the available skull of *Dicerorhinus primaevus* Arambourg (1959) from the Pontian of Wad el Hammam in Algeria is that of a young individual with milk teeth, and M<sup>1</sup> erupting, lacking the posterior portion and the premaxillaries. The skull of *Dicerorhinus caucasicus* Borissiak (1938) from the Vindobonian Chokrak beds in North Caucasus is deformed and incompletely known. Hence, only the dentition and skeleton of these forms are available for comparison.

Regarding the dentition of *Dicerorhinus leakeyi*, it is most convenient to deal with all the dental material in the East African Miocene collection that may be safely referred to *Dicerorhinus*.

Both upper incisors are preserved in the holotype skull of *D. leakeyi* and of the upper dentition no. 2, R. 1 (Pl. 4, fig. 7). The crowns are elongated anteroposteriorly, with the lateral surface convex and the medial undulating, convex in front and behind and depressed in between. The lateral surface is more worn down than the medial.

The root is transversely compressed, diminishing slightly in diameters toward its blunt apex.

There are no less than eight isolated upper incisors agreeing well in shape and size with those of *D. leakeyi*, three of which are in the British Museum (Natural History) : a left specimen marked Rs. 3, Rusinga, a right specimen marked R. 1, Rusinga, and a left specimen marked R. 11, Rusinga. The National Museum specimens consist of four from the right side : no. 109, 1949, West side of Hiwegi, Rusinga (Pl. 4, fig. 8), no. 275, 1949, Kathwanga, Rusinga, no. 81, 1950, R. 1-1a, Rusinga, and F. 3056, Kathwanga, Rusinga, and a left specimen numbered F. 3060, Rusinga. Measurements are given in Table 2.

TABLE 2  
Measurements of upper incisors of *Dicerorhinus leakeyi* (mm.)

|            | Type   |      | no. 2   |      | Rs. 3   | R. 1 | R. 11 | no. 109 | no. 275 |
|------------|--------|------|---------|------|---------|------|-------|---------|---------|
|            | dext.  | sin. | dext.   | sin. |         |      |       |         |         |
| Ant. post. | 38     | 37   | 35      | 34   | 36      | 33   | —     | 34      | —       |
| Transv.    | 18     | 18   | 16      | 15   | 14      | 15   | 14    | 15      | 15      |
|            | no. 81 |      | F. 3056 |      | F. 3060 |      |       |         |         |
| Ant. post. | —      |      | 32      |      | 32      |      |       |         |         |
| Transv.    | 14     |      | 15      |      | —       |      |       |         |         |

The root is well preserved in most specimens, varying from 3.5 to 4 cm. in length. The amount of individual variation within this series is not very great. A very much larger upper incisor from Rusinga will be dealt with below under *Brachypotherium*.

The upper incisors of *D. schleiermacheri* (Kaup 1834 : 34, pl. 11, figs. 3, 4) are similar in crown size to those of *D. leakeyi* : diameters 35 by 16 mm. and 33 by 13 mm., but the root appears to be more massive in the Eppelsheim species. Moreover, there is a small second incisor behind the larger one in each premaxillary, 8 mm. in diameter (Kaup 1834 : 34) ; of these there is no trace in the Rusinga skull. In *D. orientalis* the upper incisors have not been found, and from the tapering (incomplete) premaxillaries it may be concluded that they were either reduced or absent. The same applies to *D. ringstroemi*.

The foremost teeth present in the holotype skull *D. leakeyi* are the first upper milk molars, DM<sup>1</sup>. They are, however, too worn and damaged to reveal much of their structure ; the milk dentition of *Dicerorhinus* will be dealt with later.

The upper premolars P<sup>2-4</sup> of the type skull of *D. leakeyi* as well as those of the dentition no. 2, R. 1 (Pl. 2, fig. 3, Pl. 5, figs. 2, 3), (P<sup>2</sup> sin. is not preserved) are much worn down. The external surface of the left P<sup>2</sup> and P<sup>4</sup> as well as that of the right P<sup>3</sup> in the type skull are incomplete, and the right P<sup>2</sup> and P<sup>3</sup> are incomplete internally. P<sup>2</sup> is worn to such a degree that a small portion of the medisinus only remains on the occlusal surface. P<sup>3</sup> and P<sup>4</sup> both have protoloph and metaloph connected internally forming a high lingual wall up to at least 12 mm. (P<sup>3</sup>) or 15 mm. (P<sup>4</sup>) above the enamel

base; the teeth are worn down to this level. There is a weak cingulum on the internal surface, 8 mm. high on the proto-loph, and slowly rising behind. In the least worn premolar ( $P^4$ ) the lingual third of the medisinus, well cut off from the internal wall, and the postsinus are shown on the worn surface. The internal surface of the crowns of  $P^3$  and  $P^4$  has a weak vertical depression at the junction of proto-loph and metaloph; the protocone is only weakly constricted off.

There are various isolated upper premolars, all much worn, that should be referred to *Dicerorhinus*, viz.,

No. 752, 1951, Rusinga,  $P^2$  sin., incomplete postero-internally,

No. 1385, 1951, Rusinga,  $P^3$  dext. (Pl. 6, fig. 12),

No. 2549, 1952, Rusinga,  $P^3$  sin., damaged behind, and

No. 80, 1950, R. 1-1a, Rusinga,  $P^4$  dext.

These specimens all have the high internal wall of the *Dicerorhinus* type; the internal cingulum is hardly visible in some specimens. Measurements have been entered in Table 3.

TABLE 3

Measurements of upper premolars of *Dicerorhinus leakeyi* (mm.)

|                    | Type | no. 2 | no. 752 |          |          |
|--------------------|------|-------|---------|----------|----------|
| $P^2$ , ant. post. | 26   | 31    | 29      |          |          |
| ant. transv.       | 34   | 35    | 35      |          |          |
| post. transv.      | 36   | 37    | —       |          |          |
|                    |      |       |         | no. 1385 | no. 2549 |
| $P^3$ , ant. post. | 29   | 33    | 31      | —        | —        |
| ant. transv.       | 43   | 46    | 46      | 47       | 47       |
| post. transv.      | 44   | —     | 43      | —        | —        |
|                    |      |       |         | no. 80   |          |
| $P^4$ , ant. post. | 31   | 38    | 34      |          |          |
| ant. transv.       | 51   | 50    | 52      |          |          |
| post. transv.      | 49   | 47    | 49      |          |          |

The upper molars of the holotype skull of *Dicerorhinus leakeyi* are characterized by their low and wide lingual medisinus entrances. All except  $M^2$  dext. lack portions of the external surface, while  $M^1$  dext. is incomplete antero-internally as well. The molars of the upper dentition no. 2, R. 1, Rusinga (only those from the right side are preserved), are very similar to those of the holotype and worn to a slightly less degree; the  $M^2$  is incomplete antero-externally and  $M^3$  is incomplete behind. There is no manifestation of a lingual cingulum in the molars except for a small tubercle at the medisinus entrance of the  $M^1$  in no. 2. The medisinus is not blocked by the antecrochet, which is hardly visible; the protocone is not or hardly constricted. The crochet is weak and there is no crista. The ectoloph is much depressed between the roots.

The  $M^3$  has a character that lends it a primitive look, viz., the bulging out of the outer surface at the junction of ectoloph and metaloph. This bulge, representing the metacone and supported by a heavy postero-external root, gives the crown a trapezoid, somewhat  $M^1$ - $2$ -like outline quite different from the nearly triangular outline found in the  $M^3$  of *Aceratherium acutirostratum* (Deraniyagala) (Hooijer 1963, pl. 7, fig. 1), in which ectoloph and metaloph are confluent without a bulge to mark their junction. In this character the  $M^3$  of *Dicerorhinus* is definitely more primitive than that of *Aceratherium*.

The projection of the metastyle and posterior half of the metacone in  $M^3$  is lost early in the history of the Rhinocerotidae, as fully discussed by Wood (1927). In the Eocene *Hyrachyus* (Wood 1934, pl. 22) there is a marked posterior projection of the metacone and metastyle in  $M^3$ . This projection is no longer discrete in *Dicerorhinus*, having merged into the outer surface, but the basal bulge is still there.<sup>1</sup>

It is interesting to note that in Recent *Dicerorhinus sumatrensis*  $M^3$  shows the same development: ectoloph and metaloph, although confluent, form a wide angle with a basal bulge (Hooijer 1946a, pl. 2, fig. 8, pl. 3, fig. 1).

There are numerous isolated upper molars in the East African Miocene collection that present the *Dicerorhinus* type, as follows:

No. 1163, 1950, R. 1, Rusinga,  $M^1$  sin., ectoloph incomplete,

No. 1161, 1950, R. 1, Rusinga,  $M^2$  sin. (Pl. 6, fig. 7),

No. 82, 1950, R. 1-1a, Rusinga,  $M^1$  sin. without parastyle and metastyle,

No. 37, 1947, Songhor, anterior outer fragment of left upper molar,

No. 485, 1948, Kathwanga, Rusinga,  $M^3$  dext., outer and anterior parts lost,

No. 14, 1949, R. 1, Rusinga,  $M^3$  dext.,

No. 711, 1949, Gumba, Rusinga,  $M^3$  dext., much worn, outer surface broken off, two unnumbered portions of  $M^3$  sin., Rusinga, one much worn down and with the enamel incomplete anteriorly, the other the posterior portion only,

No. 1162, 1950, R. 1, Rusinga,  $M^3$  sin., corroded enamel and incomplete behind.

The following specimens are in the British Museum (Natural History):

$M^1$  dext., R. 1, Rusinga, lacking metastyle,

$M^2$  dext., R. 2, Rusinga, metastyle and part of protoloph wanting,

$M^2$  sin., Rusinga, lacking outer portion,

$M^3$  sin., R. 1, Rusinga (Pl. 7, figs. 5, 6) and

$M^3$  dext., Rs. 108, Rusinga, lacking posterior portion, weak crista.

Measurements of these specimens are presented in Table 4.

In a collection from Napak, Karamoja, Uganda, entrusted to me by Dr. W. W. Bishop, there is the anterior surface of the protoloph of a left upper molar (no. 509, Napak VI, 1961 (1)) with a very weak protocone fold that I have no doubt should be referred to *Dicerorhinus*. It can be exactly duplicated in the Rusinga material listed above.

<sup>1</sup> Recently Wood (1963) described a primitive true rhinoceros from the Late Eocene of Mongolia as *Pappaceras confluens*, the specific name referring to the essentially confluent ectoloph and metaloph of  $M^3$ , a rather advanced structure in such an early Tertiary form.

TABLE 4

Measurements of upper molars of *Dicerorhinus leakeyi* (mm.)

|                             | Type | no. 2 | no. 1163 | no. 82  | R. 1     |      |         |     |
|-----------------------------|------|-------|----------|---------|----------|------|---------|-----|
| M <sup>1</sup> , ant. post. | 36   | 41    | —        | —       | 40       |      |         |     |
| ant. transv.                | 50   | 52    | 52       | 53      | 50       |      |         |     |
| post. transv.               | 46   | 49    | 49       | 49      | 47       |      |         |     |
| p. tr. : a. tr.             | 0.92 | 0.94  | 0.94     | 0.93    | 0.94     |      |         |     |
|                             |      |       | no. 1161 | R. 2    |          |      |         |     |
| M <sup>2</sup> , ant. post. | 41   | 43    | 42       | 43      |          |      |         |     |
| ant. transv.                | 55   | 55    | 54       | 55      |          |      |         |     |
| post. transv.               | 46   | 47    | 48       | 49      |          |      |         |     |
| p. tr. : a. tr.             | 0.84 | 0.85  | 0.89     | 0.89    |          |      |         |     |
|                             |      |       | no. 14   | no. 711 | no. 1162 | R. 1 | Rs. 108 | Rs. |
| M <sup>3</sup> , ant. post. | 42   | 46    | 44       | 45      | —        | 42   | —       | 43  |
| ant. transv.                | 51   | 53    | 51       | —       | c. 50    | 50   | 50      | 54  |
| l. outer surface            | 52   | —     | 55       | —       | —        | 53   | —       | 57  |

The ratio of the postero-transverse to the antero-transverse diameter shows that M<sup>2</sup> is relatively narrower behind than is M<sup>1</sup>. In M<sup>3</sup> the metacone bulge can be seen in most specimens; the M<sup>3</sup> sin. from R. 1 is entire behind and shows the bulge very well. In Recent *D. sumatrensis* the bulge is as marked: in an M<sup>3</sup> sin. from a Sumatran cave (Dubois Collection no. 910a) as in nearly all the Sumatran cave teeth, the roots have been eaten away by porcupines and only the enamel of the crown, nibbled at the edge, remains, but in basal view the trapezoid outline of the crown is well seen, corresponding with that made by the heavy rounded root of the metacone in the Rusinga tooth. The posterior width (metacone-hypocone) happens to be the same in the two specimens (37 mm.), and the antero-transverse diameter is also the same in the two (50 mm.). The posterior cingulum is somewhat better developed in the Rusinga specimen than in that from Sumatra, but this is a highly variable feature: in another Sumatran M<sup>3</sup> (Dubois Collection no. 663a) the posterior cingulum is as well developed as that in the Rusinga M<sup>3</sup>.

The upper premolars and molars of *Dicerorhinus schleiermacheri* as figured by Kaup (1834, pl. 11, fig. 5) are larger than those in the Rusinga *Dicerorhinus*; the length P<sup>2</sup>-M<sup>3</sup> is 250 mm. as figured by Kaup against 205 mm. in the holotype skull and 220 mm. in dentition no. 2 of *D. leakeyi*. The maximal transverse diameters given in the text (Kaup 1834:37) are: P<sup>4</sup> 60 mm.; M<sup>1</sup> 62 mm.; M<sup>2</sup> 65 mm., whereas in *D. leakeyi* the antero-transverse diameters are at most 52 mm. in P<sup>4</sup>, 53 mm. in M<sup>1</sup> and 55 mm. in M<sup>2</sup>. In structure, however, the Eppelsheim premolars and molars resemble those of Rusinga very closely: there is a weak internal cingulum in the premolars above which protoloph and metaloph are confluent, the protocone is weakly constricted, while in the molars the internal cingulum is absent, the mediusinus entrance low and wide, the protocone constriction weak, and M<sup>3</sup> has a bulge at the metacone base. The crista and the crochet are weak or absent in *D. leakeyi* but these projections into the mediusinus recede towards the base and hence show better

in less worn teeth such as those of *D. schleiermachi* (in various molars of *D. leakeyi* there are traces of crista and crochet). The upper dentition of *Dicerorhinus sansaniensis* (Filhol 1891 : 201, pl. 14, fig. 6 ; Pavlow 1892, pl. 5, fig. 15) agrees in characters with that of *schleiermachi* and *leakeyi* (it shows no crista and a weak crochet), but in size it is less than that of the Rusinga *Dicerorhinus* (length P<sup>2</sup>-M<sup>3</sup> 190 mm., maximal width of P<sup>4</sup> 45 mm., of M<sup>1</sup> 46 mm., and of M<sup>2</sup> 47 mm.). Hence, the upper teeth of *D. leakeyi* are intermediate in size between those of *D. schleiermachi* and *D. sansaniensis*. The upper molars available of *D. primaevus* show this to be a larger species than *D. leakeyi* : the width of M<sup>1</sup> is 57.5 mm. and that of M<sup>2</sup> 62.5 mm. (Arambourg 1959 : 59). In *D. caucasicus* the upper premolars as described by Borissiak (1938 : 9-13) have the crests internally confluent upon wear, as in *D. schleiermachi*, *D. sansaniensis* and *D. leakeyi*, but in size *D. caucasicus* is nearly as small as *D. sansaniensis* (width of P<sup>4</sup> 37 mm., of M<sup>1</sup> 51 mm., of M<sup>2</sup> 48 mm.).

The canines in the mandible of the holotype of *D. leakeyi* are subtriangular in cross-section, with rounded upper and lower outer edges and a sharp edge internally. At the base of the crown the diameters are 30 mm. horizontally and 21 mm. vertically. The distance between them amounts only to 11 mm., but between them, or rather crowded out below the inner edges of the canines there are two small incisors, round in section and with pea-shaped crowns 8 mm. in diameter. In mandible no. 2 there are only the alveoli of the incisors and canines, but they resemble those in the holotype very closely. The depth of the alveolus of the left canine, exposed laterally, is just over 10 cm. An isolated pair of lower canines thought to belong to no. 2 (Pl. 4, figs. 4, 5) have crowns agreeing exactly in shape and size with those of the type ; the crown length is 4.5 cm. and the roots, which are straight and gradually taper toward the apex, have a length of 9 cm.

The tip of a left lower canine, no. 980, 1950, Kiangata, Rusinga, is 30 mm. transversely at crown base and very nearly round in section at the root (30 mm. horizontally and 28 mm. vertically). The length of the worn crown is only 27 mm., indicating perhaps that it was less procumbent than the others. Whether this canine belongs to *Dicerorhinus* or to some other genus is uncertain. We have further the lower canines of the *Aceratherium* specimen described under that head.

The lower incisors and canines of *D. schleiermachi* are similar in size to those of *D. leakeyi* ; the diameter of the incisor alveoli is 8 mm., and those of the canine 30 mm. horizontally and 22 mm. vertically (Kaup 1834, pl. 11, fig. 8 ; there is a cast in the British Museum (Natural History), no. M.2782). In the mandible of *D. sansaniensis* there are likewise small incisors between the canines (see Filhol 1891 : 201, pl. 14, fig. 1 ; Roger 1900 : 51, pl. 1, fig. 2), diameters 6 mm., and 20 mm., respectively, smaller than in the Rusinga mandibles. In *D. orientalis* as well as in *D. ringstroemi* the lower incisors or canines are much reduced (Ringström 1924, text-figs. 14, 15 and 3, 4). In *D. primaevus* only traces of the alveoli of lower incisors have been found (Arambourg 1959 : 60), and in *D. caucasicus*, as in *D. schleiermachi* to which it may be ancestral, there are subtriangular lower canines (erupting) and two small cylindrical incisors in between (Borissiak 1938 : 16, pl. 1, fig. 4).

The lower canine described from the Miocene of the Sinda-Mohari region, Congo

(Semliki no. 527, Hooijer 1963 : 48), as possibly belonging to *Dicerorhinus* is similar to that of *D. leakeyi* although smaller (basal crown diameters 22 by 11 mm.).

All the lower premolars and molars of the holotype of *D. leakeyi* are present, including a small and slightly worn  $P_1$ . Those of dentition no. 2, R. 1, 1947, are slightly larger; only the right side of the mandible is intact and it shows no trace of a  $P_1$ , while nothing is preserved of the left ramus except the isolated  $P_4$ ,  $M_2$  (Pl. 6, fig. 8) and  $M_3$ . These teeth are characterized by having a deep vertical groove externally between the two lophids, the metalophid in front and the hypolophid behind, and by the absence of an external cingulum. There are a few more mandibles presenting the same characters, as follows:

M. 18921 is a mandible from Rusinga that has alveoli for the I and C as in the *Dicerorhinus* specimens. The teeth preserved are the right  $P_4$  and  $M_{2-3}$ , and the left  $P_3-M_3$ . The ascending portions of the rami are restored with plaster behind. The teeth present no differences from those in the holotype and no. 2.

No. 231, 1949, a right mandibular ramus from R. 2-4, Rusinga, has  $P_4$  and  $M_{2-3}$  *in situ*. The symphyseal portion is missing, and of the postdental portion only the angular process is preserved. The teeth agree with those of *Dicerorhinus* in size and characters.

Measurements are given in Table 5.

The length of the mandibular tooth-row  $P_2-M_3$  is 250 mm. in *D. schleiermacheri* and 196 mm. in *D. sansaniensis* (Kaup 1854 : 3), longer, and shorter, respectively,

TABLE 5

Measurements of lower premolars and molars of *Dicerorhinus leakeyi* (mm.).

|                    | Type | no. 2 | M. 18921 | no. 231 |
|--------------------|------|-------|----------|---------|
| $P_1$ , ant. post. | 18   | —     | —        | —       |
| transv.            | 11   | —     | —        | —       |
| $P_2$ , ant. post. | 26   | 28    | —        | —       |
| ant. transv.       | 16   | 16    | —        | —       |
| post. transv.      | 17   | 18    | —        | —       |
| $P_3$ , ant. post. | 31   | 34    | —        | —       |
| ant. transv.       | 21   | 20    | 21       | —       |
| post. transv.      | 23   | 23    | 24       | —       |
| $P_4$ , ant. post. | 35   | 37    | 35       | 36      |
| ant. transv.       | 26   | 26    | 26       | —       |
| post. transv.      | 28   | 28    | 27       | —       |
| $M_1$ , ant. post. | —    | 41    | —        | —       |
| ant. transv.       | 29   | 28    | —        | —       |
| post. transv.      | 30   | 31    | —        | —       |
| $M_2$ , ant. post. | 41   | 45    | 45       | 43      |
| ant. transv.       | 32   | 30    | 31       | —       |
| post. transv.      | 31   | 31    | 31       | 27      |
| $M_3$ , ant. post. | 44   | 51    | 49       | 44      |
| ant. transv.       | 30   | 30    | 31       | 28      |
| post. transv.      | 28   | 29    | 27       | 28      |
| Length $P_2-M_3$   | 215  | 235   | —        | 225     |

than in the *D. leakeyi* specimens (Table 5). In the figured mandible of *D. schleiermacheri* the anterior premolar  $P_1$  is absent, but it occurs in one out of twenty-four mandibles (Kaup 1834 : 37, see pl. 11, fig. 8a), and it is about 11 by 7 mm. in crown diameters. In *D. sansaniensis* a  $P_1$  is present in the figured mandible, diameters 15 by 10 mm. (Filhol 1891 : 201). In the second mandible of *D. leakeyi*  $P_1$  has not developed. It is evident that the presence or absence of this tooth is not a character of great significance.

Apart from a few isolated lower molars that have a flattened external surface and therefore belong to *Brachypotherium* there remain a number of lower jaw fragments with teeth and isolated lower teeth that have the groove externally between meta- and hypolophid. Although they are very similar in size to those of *Dicerorhinus* they do not necessarily belong to that genus. They may in part represent *Aceratherium* (the lower molars of *Aceratherium* cannot be distinguished from those of *Dicerorhinus*), and some of them may even represent *Brachypotherium* if the flattened outer groove is not constant in the Rusinga and Karungu *Brachypotherium*. However, since *Dicerorhinus* is the most common of the East African Miocene rhinoceroses, most of the lower teeth probably belong to that genus, and are enumerated below:

No. 786, 1948, West Hiwegi, Rusinga, left mandibular ramus with  $P_3$ - $M_3$ , teeth all fractured and incomplete,  $P_4$  slightly worn,  $M_3$  erupting,

No. 788, 1948, West Hiwegi, Rusinga, a right ramus, teeth broken off,

No. 1063, Kiahera Hill, Rusinga,  $P_2$  sin.,

No. 990, 1950, Gumba Rusinga,  $P_3$  dext.,

No. 1397, 1950, Rusinga,  $M_1$  dext.,

No. 223, 1949, Wakondu, Rusinga, right ramus fragment with  $M_{2-3}$ ,

No. 429, Ngira, Karungu, unerupted crowns of  $P_{2-4}$  dext., slightly worn  $M_1$  dext., and unworn incomplete crown of  $M_2$  dext.,

No. 596, 1947, junction R. 1 and R. 1a, Rusinga, left ramus with  $M_{2-3}$ ,

Five isolated teeth, all marked RS, Rusinga, representing the left  $P_4$  and the right and left  $M_{2-3}$ , all much worn down,

No. 342, 1950, Ngira, Karungu, incomplete  $P_3$  dext.,

A ramus fragment marked "Aloir, '39, Owen" bears the damaged crowns of the left  $P_4$  and  $M_1$ ,

A ramus fragment marked "Karungu, 1937, Owen" has a much worn left  $M_2$  that is incomplete externally behind,

Nos. 84-86, 1950, R. 1-1a, Rusinga, incomplete  $P_4$  and  $M_{2-3}$  dext., possibly belonging together,

F. 3062 and F. 3057 are two portions of a left lower molar from Rusinga,

No. 83, 1950, R. 1-1a, Rusinga, a much worn and incomplete  $M_1$  or  $M_2$  sin.

$M_1$  is wider behind than in front. In  $M_2$  the posterior lophid is either wider or narrower than the anterior, and in  $M_3$  either the width is greatest in front, or (no. 231 ; Table 5) there is no difference between anterior and posterior width.  $M_3$  is further characterized by the slight development of the posterior cingulum and (but this only upon a certain amount of wear) the absence of a posterior pressure scar. Measurements of the Rusinga and Karungu specimens are given in Table 6.



TABLE 6

Measurements of lower teeth from Rusinga and Karungu (mm.)

|                             | no. 786 | no. 1063 | no. 429 | RS | no. 342     | nos. 84-86 |
|-----------------------------|---------|----------|---------|----|-------------|------------|
| P <sub>2</sub> , ant. post. | —       | 27       | 28      | —  | —           | —          |
| ant. transv.                | —       | 16       | 15      | —  | —           | —          |
| post. transv.               | —       | 19       | 18      | —  | —           | —          |
|                             |         | no. 990  |         |    |             |            |
| P <sub>3</sub> , ant. post. | —       | 35       | —       | —  | —           | —          |
| ant. transv.                | —       | 20       | —       | —  | 21          | —          |
| post. transv.               | 23      | 22       | —       | —  | 23          | —          |
|                             |         |          |         |    | Aloir '39   |            |
| P <sub>4</sub> , ant. post. | 39      | —        | 38      | —  | —           | 38         |
| ant. transv.                | —       | —        | 25      | 24 | —           | —          |
| post. transv.               | 26      | —        | 27      | 27 | 25          | —          |
|                             |         | no. 1397 |         |    |             |            |
| M <sub>1</sub> , ant. post. | —       | 42       | 44      | —  | —           | —          |
| ant. transv.                | 26      | 26       | 27      | —  | —           | —          |
| post. transv.               | —       | 28       | 31      | —  | —           | —          |
|                             |         | no. 223  | no. 596 |    | Karungu '37 |            |
| M <sub>2</sub> , ant. post. | —       | 43       | —       | 42 | 47          | 45         |
| ant. transv.                | 29      | 28       | 26      | 29 | 31          | —          |
| post. transv.               | 27      | 29       | 27      | 29 | —           | 28         |
| M <sub>3</sub> , ant. post. | —       | 45       | 44      | 46 | —           | —          |
| ant. transv.                | —       | 29       | 27      | 28 | —           | 30         |
| post. transv.               | —       | 26       | 26      | 27 | —           | —          |

For the sake of completeness I mention the lower molar fragments that comprise only the hypolophid, and do not show whether the groove between it and the meta-lophid was deep or flattened. These are R. 106, Rusinga; no. 346, 1950, Ngira, Karungu; no. 446, Kachuku, Karungu, and F. 3051, Rusinga. The last two are posterior portions of M<sub>3</sub>, right and left, and 26-28 mm. wide. Nothing can of course be said as to the generic position of these fragments.

In the British Museum (Natural History) there is a set of upper milk molars, DM<sup>1-4</sup> sin., *in situ* in a maxillary, very well preserved, and marked Rs. 26, Rusinga (Pl. 5, fig. 1). DM<sup>1</sup> is a small triangular tooth the ectoloph of which bears a vertical ridge in the middle, the mesostyle. The protocone, which is placed internally at the same level as the mesostyle, is an isolated cusp. The front part of the crown narrows anteriorly and is bounded lingually by a low ridge and buccally by the ectoloph crest, which unite at the antero-external angle so as to enclose a shallow fossa. The hypocone behind the protocone is connected with the metacone by a low ridge separating the medisinus from the postsinus. DM<sup>2</sup> has a mesostyle (not present in the more

posteriorly placed milk molars or in the permanent dentition). The protoloph and the metaloph are damaged internally but appear to be equally long transversely. Both the paracone style and the metacone style are weak. The entrance to the medisinus is low and V-shaped. There is a crista united with the crochet, closing off a medifossette. DM<sup>3</sup> has no crista, and the crochet extends only half way across the medisinus. The ectoloph is depressed between the roots. The paracone style is only in part preserved and the parastyle has broken off. The medisinus entrance is wider than that in DM<sup>2</sup> and likewise unobstructed. The grooves delimiting the protocone are faintly shown. DM<sup>4</sup>, of which the paracone style is incomplete, has the valley entrance again wider, the crochet longer, but the protocone constriction as little developed as in DM<sup>3</sup>. The anterior cingulum is more prominent, but, like in DM<sup>3</sup>, it does not quite extend to the antero-internal crown angle. There is no trace of a cingulum internally. The posterior moiety of the ectoloph with the faint metacone style is much more inclined inward than the anterior half.

The DM<sup>4</sup> of the Rusinga milk dentition agrees so well with the M<sup>1</sup> of the *Dicerorhinus* dentitions from Rusinga, differing mainly in lesser size (Table 7) and thinner enamel, as may be expected, that the juvenile Rusinga specimen may also be referred to *D. leakeyi*.

TABLE 7

Measurements of upper milk teeth of *Dicerorhinus leakeyi* (mm.)

|                              |       |                              |      |
|------------------------------|-------|------------------------------|------|
| DM <sup>1</sup> , ant. post. | 24    | DM <sup>3</sup> , ant. post. | 32   |
| transv.                      | 20    | ant. transv.                 | 37   |
| DM <sup>2</sup> , ant. post. | 26    | post. transv.                | 35   |
| ant. transv.                 | c. 30 | DM <sup>4</sup> , ant. post. | 36   |
| post. transv.                | c. 30 | ant. transv.                 | 40   |
|                              |       | post. transv.                | 39   |
|                              |       | p. tr. : a. tr.              | 0.98 |

There are two specimens of DM<sup>4</sup> from Rusinga that should be referred to *Acera-therium*, and they will be dealt with later. There are also a much worn right DM<sup>1</sup> (no. 546, 1950, R. 3, Rusinga) with a length of c. 25 mm. and another DM<sup>1</sup> dext. from Rusinga that is 22 mm. wide.

The upper milk dentition of *D. schleiermacheri* as figured by Kaup (1834, pl. 11, fig. 7) is larger than that of *D. leakeyi*; the overall length of DM<sup>2-4</sup> is 120 mm. as opposed to 103 mm. in the Rusinga specimen, and the width of DM<sup>3</sup> is 40 mm., that of DM<sup>4</sup> 42 mm. (Kaup (1834 : 37) gives 52 mm. for the width of DM<sup>4</sup>, but a cast of the figured specimen in the British Museum (Natural History), no. 110b (O.C.), shows it to be 42 mm.). The crochet is better developed in the Eppelsheim milk teeth than in those from Rusinga. The milk dentition of *D. sansaniensis* (Pavlov 1892, pl. 5, fig. 8) has a length DM<sup>2-4</sup> of 104 mm., and widths of DM<sup>3</sup> and DM<sup>4</sup> of 35 and 37 mm. respectively, as measured from the figures, slightly less than in *D. leakeyi*. The milk dentition of *D. primaevus* as given by Arambourg (1959 : 59) is larger than that of *D. leakeyi* (length DM<sup>2-4</sup> 123.5-131.5 mm., width DM<sup>3</sup> 42.5-45 mm., of DM<sup>4</sup> 44-50.4

mm.). It is within these limits that falls the  $DM^4$  of *Dicerorhinus* (?) spec. from the Pontian of Gravitelli, Sicily, the width of which is 47 mm. (Hooijer, 1946c : 322).

The lower milk dentition of *Dicerorhinus leakeyi* is best represented in a specimen from Napak V (August, 1962), Uganda, sent to me for identification by Dr. W. W. Bishop. It comprises  $DM_{2-4}$  dext., with the crowns unworn; the metalophids of  $DM_3$  and  $DM_4$  are damaged apically behind. The posterior valley of  $DM_2$  is closed inside, the anterior valley of  $DM_3$  nearly so. In  $DM_3$  the metalophid is bilobed in front, the parastylid well developed (Pl. 4, fig. 1). This dentition tallies well in size with the upper milk dentition of *Dicerorhinus* from Rusinga and may be referred to the same species. There are more remains of the lower milk dentition from Karungu and Rusinga some of which present larger dimensions than the Napak specimens, but the difference is small. These are:

No. 429, Ngira, Karungu, right  $DM_3$  and part of  $DM_4$  in a ramus fragment (this number also includes the unerupted premolars evidently of the same individual),

No. 405, 1951, Rusinga, right ramus with  $DM_{3-4}$  and erupting  $M_1$ ,

No. 1580, 1950, Rusinga, part of left  $DM_3$  in ramus fragment,

F. 3058, Rusinga, posterior portion of  $DM_3$  and anterior portion of  $DM_4$  sin.,

F. 3059, Rusinga, anterior portion of  $DM_4$  dext., and

No. 485, 1948, Kathwanga, Rusinga, posterior portion of  $DM_4$  sin.

Measurements of the lower milk molars are given in Table 8.

TABLE 8

Measurements of lower milk teeth from Napak, Karungu, and Rusinga (mm.)

|                     | Napak V | no. 429 | no. 405 | no. 1580 | nos. 3058/9<br>and 485 |
|---------------------|---------|---------|---------|----------|------------------------|
| $DM_2$ , ant. post. | 27      | —       | —       | —        | —                      |
| ant. transv.        | 13      | —       | —       | —        | —                      |
| post. transv.       | 16      | —       | —       | —        | —                      |
| $DM_3$ , ant. post. | 37      | 36      | 40      | —        | —                      |
| ant. transv.        | 17      | 19      | 19      | 18       | —                      |
| post. transv.       | 20      | 21      | 21      | —        | —                      |
| $DM_4$ , ant. post. | 34      | —       | 37      | —        | —                      |
| ant. transv.        | 19      | 22      | 23      | —        | 19                     |
| post. transv.       | 20      | —       | —       | —        | 20                     |

$DM_2$  in *D. schleiermachersi* (Kaup 1834 : 38, pl. 11, fig. 10) measures 28 mm. antero-posteriorly and 15.5 mm. in width; it has the posterior valley closed inside. The various milk dentitions of *D. primaevus* (Arambourg 1959 : 63) are larger than the East African  $DM_{2-4}$  except in the width of  $DM_2$  which is given as 13.5–15 mm.; the width of  $DM_3$  is 22–26 mm., and that of  $DM_4$  23.5–26.5 mm. The posterior valley of  $DM_2$  is open inside, making it a narrow tooth in *D. primaevus*, but as observed by

Arambourg (1959 : 62) the valley may be either open or closed in  $DM_2$  of *D. schleiermacheri*, and this varies in the Recent species also : the posterior valley in  $DM_2$  becomes either shallower or deeper as it passes outwards. In the latter case it may become isolated as an enamel island upon wear and show a lingually closed valley (Hooijer 1946a : 32).

Genus *ACERATHERIUM* Kaup 1832

*Aceratherium acutirostratum* (Deraniyagala)

(Pl. 3 ; Pl. 4, figs. 2, 3 ; Pl. 5, figs. 4, 5 ; Pl. 6, figs. 1-4 ; Pl. 9, figs. 2-4 ;  
Pl. 14, figs. 4, 5)

1951a *Turkanatherium acutirostratus* Deraniyagala : 24.

1951 *Turkanatherium acutirostratus* Deraniyagala : 134, pl. 1.

1953 *Turkanatherium acutirostratus* Deraniyagala ; Deraniyagala : 13, pl. 1 ; pl. 2, figs. b, c ;  
pl. 3, figs. b, d.

The skull from Moruaret Hill near Losodok described by Deraniyagala (1951, 1953) as *Turkanatherium acutirostratus* has elongate, weak nasals and a weak double sagittal crest. There is neither a nasal nor a frontal horn. The premaxillaries are well developed and, although incomplete, extend forward beyond the nasals. They evidently carried incisors, but these are lacking. The occiput is elevated, giving a concave fronto-parietal profile. The dentition of the Turkana skull is characterized by the antecrochet blocking the medisinus in the premolars, which have a prominent internal cingulum, and a markedly constricted protocone and strong antecrochet in the molars. These are characters occurring in *Aceratherium*, and I have recently described a number of teeth from the Miocene of Congo as *Aceratherium acutirostratum* (Deraniyagala) (Hooijer 1963 : 43, pl. 6, figs. 1-3 ; pl. 7, figs. 1, 3-5, 8 ; pl. 8, fig. 2). Earlier, Arambourg (1959 : 74) had already stated that *Turkanatherium* appeared to be a synonym of *Aceratherium*.

There are various *Aceratherium* species in the Tertiary of Europe known by more or less complete skulls, and the Turkana *Aceratherium* may be compared with these. The high occiput is found only in the Pontian *Aceratherium incisivum* (Kaup 1834, pl. 10, fig. 2) ; in the earlier species the occiput is less elevated (see Wang 1928, text-fig. 1). *Aceratherium incisivum*, as first discovered by Osborn (1899), has a frontal horn, of which there is no evidence in *Aceratherium acutirostratum* or in the pre-Pontian European species. Elongate weak nasals are common in *Aceratherium* ; those in the Turkana skull appear to agree best with those of *Aceratherium lemanense* (Pomel) (Mermier 1896, pl. 1). In this Stampian and Aquitanian species the nasomaxillary notch extends backward only to above the middle of  $P^3$ , as in the Turkana skull ; in *Aceratherium platyodon* Mermier of the Burdigalian and in *Aceratherium tetradactylum* (Lartet) of the Vindobonian the notch extends backward to above the middle of  $P^4$ , whereas in *A. incisivum* it extends to above the front of  $M^1$  (Mermier 1896, pl. 1 ; Breuning 1924 : 13). In the Turkana skull the anterior border of the orbit is above the anterior border of  $M^2$ , as in *A. lemanense*, *A. platyodon*, and *A. tetradactylum* ; in *A. incisivum* it is above the middle of  $M^2$  (Mermier 1896, pl. 1).

*Aceratherium lemanense* has a true sagittal crest (skull from Gannat figured by Roman 1912, pl. 8, figs. 1, 1a) as well as one of the *Aceratherium incisivum* skulls (Kaup 1834 : pl. 10, fig. 2a) ; in the other skull of *A. incisivum* (Kaup 1834, pl. 10, fig. 2b) the fronto-parietal crests do not meet.

In the collection from R. 1, Rusinga, there are remains of an *Aceratherium* skull, numbered 850, 1947. Unfortunately the skull is in fragments, and it has been possible only to assemble the nasals (Pl. 9, fig. 3) and the fronto-parietal portion of the skull, not fitting together. In restoring these from the fragments both parts appeared to be distorted by pressure mostly from the right side. The nasals evidently did not carry a horn : there is no eminence or rugosity but a groove in the median line instead. The length from the tip to the beginning of the downward curve for the nasomaxillary notch is 14 cm. ; the width of the nasals from 5 cm. behind the blunt tip backward to the narial notch is only 8 cm. throughout. Thus, the nasals are long and slender, as in *A. lemanense*. The fronto-parietal portion shows at least the absence of a true sagittal crest ; the least distance between the two fronto-parietal crests is  $4\frac{1}{2}$  cm., as in one of the *A. incisivum* skulls referred to above. There are no indications of the presence of a frontal horn in the Rusinga skull. Neither the greatest width at the postorbital processes nor the dorsal profile can be made out from the Rusinga specimen.

Of the upper dentition of skull no. 850 only a few fragments remain, and they do not show any characteristic features except for one that shows a pit inside the cingulum at the medisinus entrance ; all the crown fragments are much worn down. The mandible of the skull is preserved, but much fragmented and distorted. The symphyseal portion is poorly preserved, and the canine alveoli cannot well be traced. The rami are incomplete below, and nothing is preserved of the postdental portions except for the tip of the left coronoid process. The dentition,  $P_3-M_3$  of both sides, is well worn down, and will be dealt with later.

The upper dentition of *Aceratherium* is less well represented at Rusinga than is that of *Dicerorhinus* ; there are, however, a few characteristic premolars. Two specimens, nos. 231 and 232, 1950, R. 2-4, Rusinga, comprise a  $P^4$  dext. with part of the  $M^1$  attached to it, and a  $P^4$  sin. of the same individual. The antero-external corners of both premolars are broken off (Pl. 6, figs. 1-4). The  $P^4$  is worn down slightly less than in the *Dicerorhinus* dentitions, viz., to 16 mm. from the internal enamel base (the  $M^1$  is worn down to 10 mm. ; it erupts earlier than the  $P^4$ ). There are marked differences between the  $P^4$  of nos. 231-232 and those of *Dicerorhinus*. The inner entrance to the medisinus is much lower in nos. 231-232, obstructed only by a ridge 8 mm. high, forming part of the inner cingulum, slightly rising behind and bordering a shallow pit. The bottom of the medisinus, which is only 7 mm. above the internal base of the enamel of the crown just inside the cingulum, rises inside the tooth (toward the external side) over a horizontal distance of 12 mm. to a level of 16 mm. above the enamel base. At this point the antecrochet extends completely across the medisinus. Buccally of the antecrochet the medisinus deepens again, and changes its course from transverse to obliquely forward and outward. The constriction of the protocone by anterior and posterior grooves is very marked.

The differences may be tabulated as follows :

| <i>Dicerorhinus</i> P <sup>4</sup>  | <i>Aceratherium</i> P <sup>4</sup>  |
|---|---|
| proto- and metaloph united internally up to at least 15 mm. from crown base ; internal cingulum weakly developed ; protocone constriction slight. | medisinus open lingually to 7 mm. from crown base ; internal cingulum prominent, forming ledge between proto- and metaloph ; marked protocone constriction ; antecrochet prominent. |

The type of P<sup>4</sup> represented in the sample nos. 231-232 is that of *Aceratherium acutirostratum* as described and figured from the Miocene of the Western Rift, Congo (Hooijer 1963 : 43, pl. 6, figs. 1-3 ; pl. 8, fig. 2). The Congo P<sup>4</sup> is less worn than the Rusinga specimens, and somewhat larger. It has a more developed internal cingulum, a ridge about 12 mm. high, at which level the medisinus opens internally, and extending along the protoloph, too. Some 14 mm. inside the tooth the medisinus is blocked completely by a narrow antecrochet. The constriction of the protocone is marked.

The following premolars should also be referred to *Aceratherium* :

No. 991, 1950, Gumba, Rusinga, P<sup>2</sup> sin., external portion missing ; heavy cingulum internally,

Two specimens in the British Museum (Natural History), one marked Rs.91, Rusinga, P<sup>3</sup> dext., slightly worn, inner cingulum only at medisinus entrance, narrow antecrochet across the medisinus, and the other a much worn P<sup>3</sup> sin. from R.1, Rusinga, with internal cingulum almost absent but antecrochet across medisinus,

F.3054 and F.3063 (one specimen), Rusinga, P<sup>3</sup> dext., worn and incomplete but showing the pit inside the inner cingulum at medisinus entrance,

No. 187, 1947, South of Kiahera Hill, Rusinga, P<sup>3</sup> dext., worn and corroded, showing protocone constriction and antecrochet across medisinus,

K.343, 1950, Ngira, Karungu, a P<sup>3</sup> or P<sup>4</sup> dext., sides broken off except internally, showing pit inside cingulum.

Measurements are given in Table 9.

TABLE 9

Measurements of upper premolars of *Aceratherium acutirostratum* (mm.)

|                             | Lake Albert, |              |        |      |
|-----------------------------|--------------|--------------|--------|------|
|                             | Congo        | nos. 231-232 | Rs. 91 | R. 1 |
| P <sup>3</sup> , ant. post. | —            | —            | —      | 32   |
| ant. transv.                | —            | —            | —      | 46   |
| post. transv.               | —            | —            | 38     | 42   |
| P <sup>4</sup> , ant. post. | 46           | —            | —      | —    |
| ant. transv.                | 60           | —            | —      | —    |
| post. transv.               | 53           | 46           | —      | —    |

The upper molars of *Aceratherium acutirostratum* from Lake Albert, Congo (Hooijer

1963 : 43, pl. 7, figs. 1, 3-5, 8) are larger than those of *Dicerorhinus leakeyi* and differ in the protocone being markedly constricted off. Immediately external to the posterior protocone fold the antecrochet bulges out and basally extends all across the medisinus as seen in the figured M<sup>1</sup>. This is not the case in *Dicerorhinus*. The anterior cingulum is strongly developed and encroaches upon the internal surface of the protoloph. The M<sup>3</sup> differs from that of *Dicerorhinus* in that the metacone bulge is not developed, making the crown triangular rather than trapezoid, and in the protocone being markedly constricted. The Congo M<sup>3</sup> is unworn at the paracone, and the height of the crown at this point (49 mm.) is much less than the length of the outer surface (65 mm.), making this a brachyodont tooth (cf. Cooper 1934 : 575-581). No unworn M<sup>3</sup> of *Dicerorhinus leakeyi* is available, but from the amount of crownward convergence of the parastyle and metastyle the relative height of the external surface does seem to be much the same as that in *Aceratherium acutirostratum*.

Upper molars of *Aceratherium* from Rusinga comprise three specimens only:

No. 231, 1950, R.2-4, Rusinga, anterior portion of M<sup>1</sup> dext. adhering to P<sup>4</sup> (Pl. 6, figs. 3, 4),

No. 1630, 1950, Rusinga, upper M. dext., damaged on all sides but medisinus complete, and

No. 515, 1951, Rusinga, upper M sin., ectoloph and most of metaloph missing.

Among the rhino material from Napak, Karamoja, Uganda, sent to me by Dr. W. W. Bishop there is a specimen (no. 502, Napak I, 1958 (13)) showing the inner portion of the protoloph of a right upper molar with a deep protocone fold and an antecrochet all across the medisinus. This specimen represents the *Aceratherium* from Congo and Kenya.

Of the upper molars from Rusinga no measurements can be given, but some of the premolars are smaller than those from Congo. All are, however, characterized by the antecrochet extending all across the medisinus. The inner cingulum is stronger in some than in others. This varies among the European species of *Aceratherium* also.

In the British Museum (Natural History) there is a cast of a left upper dentition of *Aceratherium lemanense* from Auvergne (M.29624). I have compared this with upper dentitions of *Aceratherium incisivum* in the same museum, viz., a cast of the skull figured by Kaup (1834, pl. 10, fig. 2) with the teeth well preserved (M.2781), a left P<sup>2</sup>-M<sup>3</sup> (Enniskillen collection, M.233), a left P<sup>2-4</sup> (Hastings collection, M.27464), and an isolated M<sup>3</sup> dext. (Enniskillen collection, M.2370). All are from Eppelsheim. As shown in Table 10 the dentition of *A. lemanense* is similar in size to those of *A. incisivum*, but the postero-transverse diameter of M<sup>1</sup> and M<sup>2</sup> is equal to the antero-transverse diameter, and M<sup>3</sup> is relatively larger. Other primitive characters shown in the *A. lemanense* dentition are the stronger inner cingulum and the absence of crista and crochet. In both, however, we find the strong antecrochet and protocone constriction typical of *Aceratherium* molars. The crista is variously developed in *A. incisivum*: there are traces in P<sup>3</sup> and P<sup>4</sup> in M.2781 and M.233; it is more developed in M.27464, even forming a medifossette with the crochet in P<sup>2</sup>. In the figured dentition (Kaup 1834 : pl. 14, fig. 5) there is a medifossette in P<sup>4</sup> as well. The crochet is well developed in the molars, and in M.2370 even forms a medifossette with the

crista. The internal cingulum of the premolars either is confined to the medisinus entrance or extends forward and backward from this point.

TABLE 10  
Measurements of upper teeth of *Aceratherium* (mm.)

|                             | <i>A. lemanense</i> |         | <i>A. incisivum</i> |          |
|-----------------------------|---------------------|---------|---------------------|----------|
|                             | M. 29624            | M. 2781 | M. 233              | M. 27464 |
| P <sup>2</sup> , ant. post. | 31                  | 31      | 32                  | 26       |
| ant. transv.                | 40                  | 42      | 39                  | 35       |
| post. transv.               | 42                  | 45      | 43                  | —        |
| P <sup>3</sup> , ant. post. | 34                  | 34      | 37                  | 31       |
| ant. transv.                | 52                  | 54      | 53                  | 47       |
| post. transv.               | 50                  | 53      | 51                  | 44       |
| P <sup>4</sup> , ant. post. | 39                  | 35      | 38                  | 37       |
| ant. transv.                | 56                  | 59      | 52                  | 51       |
| post. transv.               | 53                  | 56      | 49                  | 46       |
| M <sup>1</sup> , ant. post. | 39                  | 41      | 42                  |          |
| ant. transv.                | 55                  | 60      | 54                  |          |
| post. transv.               | 55                  | 57      | 49                  |          |
| p. tr. : a. tr.             | 1.00                | 0.95    | 0.91                |          |
| M <sup>2</sup> , ant. post. | 43                  | 44      | 45                  |          |
| ant. transv.                | 58                  | 63      | 58                  |          |
| post. transv.               | 58                  | 60      | —                   |          |
| p. tr. : a. tr.             | 1.00                | 0.94    | —                   | M. 2370  |
| M <sup>3</sup> , ant. post. | 47                  | 44      | 44                  | 44       |
| ant. transv.                | 58                  | 59      | 51                  | 55       |
| l. outer surface            | 65                  | 61      | 57                  | 56       |

The *Aceratherium* dentition from Congo certainly resembles that of *A. incisivum* more than that of *A. lemanense*; there is a well-developed crochet, and at least a trace of a crista in P<sup>4</sup>, the M<sup>1</sup> and M<sup>2</sup> are narrower behind than in front (ratios 0.90 and 0.89, respectively), and M<sup>3</sup> is less wide than M<sup>2</sup> (Hooijer 1963 : 43). However, not all of the *A. lemanense* dentitions are as primitive-looking as that mentioned above, and even the antecrochet is not constant. The latter is well developed across the medisinus in the premolars of the dentition from Cindré (Allier) figured by Roman (1912 : 59, pl. 8, fig. 2a), but may be much reduced or absent as in the dentitions figured by Osborn (1900 : 242, text-fig. 8B) and by Viret (1929 : 258, pl. 27, fig. 2). Again, the prominent antecrochet blocking the medisinus in the premolars is seen in "*Teleoceras aquitanicum*" Repelin (1917 : 37, pl. 5, figs. 7, 8), which is probably the same as *A. lemanense* (Wang 1928 : 207), as well as in the Burdigalian *Aceratherium platyodon* (Mermier 1896, pl. 2, fig. 4), but it is absent in the premolars of "*Teleoceras aginense*" Repelin (1917 : 12, pls. 1, 3, 4), which, as pointed out by Lavocat (1951 : 114) is identical with *Aceratherium lemanense*. Also, the first and second molars of *A. lemanense* are not always as wide behind as in front as seen from the figures cited. In *A. tetradactylum* we find much variation in tooth size, development of antecrochet in the premolars, and the inner cingulum (Wang 1928 : 189). The teeth of this



Vindobonian species are close to those of the Pontian *A. incisivum* with which it has often been united.

The lower canines numbered 850, 1947 (R. 1) (Pl. 4, figs. 2, 3) belong to the same individual and differ from those of *Dicerorhinus* in being curved, with the convex sides facing each other. The diameters at crown base are 32 mm. horizontally and 24 mm. vertically. The cross-section is a transverse oval, and the diameters of the root are 28 by 23 mm. This pair agrees with *Aceratherium* in curvature and cross-section; the root length is over 11 cm., more than in a specimen of *A. tetradactylum* from Georgensgmünd recorded by Wang (1928 : 189, text-fig. 2A) that has nearly the same diameters. In *A. incisivum* (Kaup 1834 : 52, pl. 14, fig. 9) the lower canines are much larger (length 27–30 cm., width 38–44 mm.), and very large lower C are also known in the Aquitanian *A. lemanense* (Repelin 1917 : 24, pl. 5, fig. 3). The flattening of the canine in *A. acutirostratum* is less marked than in *A. platyodon* (Mermier 1895, text-fig. 5) but more than in *A. incisivum* (Mermier 1895, text-figs. 6–8).

The only premolars and molars of the lower jaw that may be referred to *Aceratherium acutirostratum* are those in the poorly-preserved mandible numbered 850, 1947, belonging to the skull remains mentioned above (Pl. 9, fig. 4). The teeth are much worn down, devoid of external cingula and with a sharp groove between meta- and hypolophid. They cannot be distinguished from those of *Dicerorhinus leakeyi* (Table 5) but P<sub>3</sub>, M<sub>2</sub> and M<sub>3</sub> are slightly longer. In Table II the Rusinga teeth may be compared for size with those of *A. tetradactylum* (no. 1 after Filhol 1891 : 204 (Sansan), nos. 2–4 after Wang 1928 : 190 (Georgensgmünd), and no. 5 after Rinnert 1956 : 33 (Viehhausen)). The lower teeth of *A. incisivum* recorded by Kaup (1834 : 53, pl. 14, fig. 9) are not very large either.

TABLE II

Measurements of lower teeth of *Aceratherium* (mm.)

|                                       | <i>A. acutirostratum</i><br>no. 850 | <i>Aceratherium tetradactylum</i> |     |      |     |      | <i>A. incisivum</i> |
|---------------------------------------|-------------------------------------|-----------------------------------|-----|------|-----|------|---------------------|
|                                       |                                     | 1                                 | 2   | 3    | 4   | 5    |                     |
| P <sub>3</sub> , ant. post.           | 36                                  | 31                                | 33  | 30·5 | 30  | 32   | 30                  |
| ant. transv.                          | 20                                  | 23                                | 20  | 14   | 16  | 18   | —                   |
| post. transv.                         | 22                                  | —                                 | 15  | 21   | 21  | 20·5 | 26                  |
| P <sub>4</sub> , ant. post.           | —                                   | 36                                | 36  | 33   | 35  | 34   | 33·5                |
| ant. transv.                          | 25                                  | 27                                | 23  | 25   | 22  | 22   | —                   |
| post. transv.                         | 26                                  | —                                 | 18  | 26   | 23  | 24   | 26                  |
| M <sub>1</sub> , ant. post.           | —                                   | 37                                | 37  | 34   | 35  | 37·5 | 34                  |
| ant. transv.                          | 26                                  | 27                                | 20  | 23   | 22  | 24·8 | —                   |
| post. transv.                         | 29                                  | —                                 | —   | 27   | 26  | 25·6 | 25                  |
| M <sub>2</sub> , ant. post.           | 48                                  | 40                                | 38? | 42   | 37  | 40·5 | 34                  |
| ant. transv.                          | 30                                  | 29                                | 22  | 25   | 25  | 27   | 26                  |
| post. transv.                         | 31                                  | —                                 | —   | 27   | 25  | 27·2 | —                   |
| M <sub>3</sub> , ant. post.           | 53                                  | 42                                | 38  | 43   | 47  | 42   | 39                  |
| ant. transv.                          | 30                                  | 27                                | 19  | 25   | 22  | 28   | 25                  |
| post. transv.                         | 29                                  | —                                 | 20  | 26·5 | 24  | 28   | —                   |
| Length P <sub>2</sub> –M <sub>3</sub> | c. 240                              | 215                               | —   | 216  | 220 | —    | 205                 |

Of the milk dentition of *Aceratherium acutirostratum* there are two specimens, both DM<sup>4</sup>: no. 142, 1949, Kamasengere, Rusinga, DM<sup>4</sup> dext. (Pl. 5, fig. 4), and no. 218, 1948, R. 107, Rusinga, DM<sup>4</sup> sin (Pl. 5, fig. 5). They differ from their homologue in the *Dicerorhinus* dentition from Rs.26 in having the protocone well defined. The anterior cingulum extends to the internal angle of the crown, the antecrochet is conspicuously developed, and the crochet is smaller. The parastyle is broken off in no. 218. These milk molars agree so closely with M<sup>1</sup> of *Aceratherium acutirostratum* in their antecrochet and cingular development and in the degree of individualization of the protocone that they may safely be regarded as *Aceratherium*. They are also larger than the *Dicerorhinus* DM<sup>4</sup> as will be seen by comparing Table 12 with Table 7.

TABLE 12

Measurements of upper milk molars of *Aceratherium acutirostratum* (mm.)

|                              | no. 142 | no. 218 |
|------------------------------|---------|---------|
| DM <sup>4</sup> , ant. post. | 40      | 38      |
| ant. transv.                 | 47      | 48      |
| post. transv.                | 45      | 44      |
| p. tr. : a. tr.              | 0.95    | 0.92    |

Genus **BRACHYPOTHERIUM** Borissiak 1927

***Brachypotherium heinzeli*** Hooijer

(Pl. 4, fig. 6 ; Pl. 6, figs. 5, 6, 9 ; Pl. 7, figs. 3, 4 ; Pl. 8 ; Pl. 9, fig. 1 ; Pl. 10, figs. 1-3, 6-8 ; Pl. 14, fig. 3)

1963 *Brachypotherium heinzeli* Hooijer : 45, pl. 6, figs. 4-6 ; pl. 8, fig. 1.

A right upper incisor, no. 79, 1950, R. 1-1a (Pl. 4, fig. 6) lacks only a portion of the root. The crown diameters are 78 mm. anteroposteriorly and 24 mm. transversely. The root is hardly higher than the crown length. This specimen, much larger than the upper I referred to *Dicerorhinus leakeyi* (Table 2), agrees well with an upper incisor of *Brachypotherium goldfussi*<sup>1</sup> (Kaup 1854 : 2, pl. 1, fig. 13 : 81 by 26 mm.), which also has a short massive root. Large incisors referred to *Aceratherium incisivum* (Kaup 1834 : 51, pl. 14, figs. 1-4 ; 1854 : 9, pl. 1, figs. 6-9) have the root higher than the crown length. If this differential character may be relied upon, the Rusinga incisor should be referred to *Brachypotherium*. Such large upper incisors have also been found at the type site of *Brachypotherium heinzeli* (Sinda no. 15) and another site, Lake Albert no. 446, from which a characteristic tooth of this species has been derived (Hooijer 1963 : 47, pl. 7, fig. 2).

There are two sets of P<sup>3-4</sup> from Rusinga that should be referred to the present

<sup>1</sup> This Pontian Eppelsheim *Brachypotherium* is considered merely a large variety of *B. brachypus* (Lartet) of the Vindobonian by Depéret (1887 : 226). The upper incisor figured with the dentition of *B. brachypus* by Depéret (1887, pl. 23, fig. 3) has a slender and long root. It has been considered probably referable to *Aceratherium* by Rinnert (1956 : 38), and is placed with "*Dicerorhinus*" (= *Aceratherium*) *simorreensis* (Lartet) by Viret (1961 : 67).

species, viz., no. 270, 1949, R. 73, Rusinga, P<sup>3-4</sup> dext. (Pl. 8, figs. 5, 6), and no. 409, 1947, West side of Hiwégi, Rusinga, P<sup>3-4</sup> sin. (Pl. 8, figs. 3, 4).

The Rusinga premolars of *Brachypotherium* agree with the type of *B. heinzellini* Hooijer (1963 : 45, pl. 6, figs. 4-6 ; pl. 8, fig. 1) in the flattening of the ectoloph behind the paracone style (the metastyle of P<sup>4</sup> in no. 270 is missing), in the development of the inner cingulum (weaker in no. 409 than in no. 270 in which latter it forms a ridge and not a mere tubercle), and in the slight development of the antecrochet, which does not block the medisinus. The external cingulum, however, so markedly developed in the holotype, is only weak in no. 409, and virtually absent in no. 270. Variations in the development of the external cingulum have been noted in *B. brachypus* also (Viret 1961 : 69).

An isolated P<sup>4</sup> sin. originating from Napak IIC, Karamoja, Uganda, collected and sent to me by Dr. W. W. Bishop in 1964, unmistakably belongs to *Brachypotherium heinzellini*. The specimen (Pl. 8, fig. 1) has the crown surface broken and distorted externally and behind the medisinus, but the protoloph is well preserved, showing the weakly developed antecrochet and the tubercle at the medisinus entrance in which it agrees perfectly with the type P<sup>4</sup>. The damage to the ectoloph notwithstanding it is clear that there was no external cingulum (well developed in the holotype, weak or absent in the Rusinga P<sup>4</sup>). The basal diameters that can be exactly taken (Table 13) are intermediate between those of the two Rusinga P<sup>4</sup>.

Neither in P<sup>3</sup> nor in P<sup>4</sup> of *B. heinzellini* the antecrochet is as strongly developed as in *B. aurelianense* (Nouel) of the Burdigalian (see Osborn 1900 : 250, text-fig. 11 ; Mayet 1908 : 100, text-fig. 29, pl. 1, figs. 1, 3<sup>1</sup>). In *B. brachypus* of the later Vindobonian the antecrochet in P<sup>3-4</sup> is reduced or wanting (Osborn 1900 : 25), although the upper dentition of *B. brachypus* from La Grive Saint-Alban figured by Depéret (1887, pl. 23) is only slightly worn and therefore does not show much of the antecrochet, which becomes more marked toward the base as seen in the right upper molar figured (Depéret 1887, pl. 23, fig. 2). The external cingulum, absent in *B. aurelianense*, is either present or reduced in *B. brachypus* (Viret 1961 : 69). The criterion of the internal cingulum, present in *B. brachypus* and weak or absent in *B. aurelianense*, is not absolute (Viret 1961). As we shall see further on, the external cingulum is either present or absent in the upper molars of *B. heinzellini*.

The first and second upper molars of *Brachypotherium* are rare in the East African Miocene. There is a much worn M<sup>1</sup> dext. from Karungu, 1937 (Pl. 6, figs. 5, 6) that has the characteristic, if not constant, feature of the species, the external cingulum. The M<sup>2</sup> sin. from the Sinda area, Lower Semliki, Congo, described and figured by me as *Aceratherium* cf. *tetradactylum* (Lartet) (Hooijer 1963 : 44, pl. 8, figs. 4-6) belongs here, too. It does lack the external cingulum, and has been identified thus because of its marked resemblance to certain large molars from Beaugency and Pontlevoy figured by Mayet (1908 : 96, 271, pl. 3, fig. 7 ; pl. 10, fig. 4) as *Aceratherium* aff. *tetradactylum*, and *Aceratherium tetradactylum* mut. *pontileviensis*, respectively. However at the time I overlooked the fact that Stehlin (1925 : 108) had referred these to

<sup>1</sup> And also Mayet 1908 : 100, text-fig. 30 : *Diceratherium douvillei* Osborn that would be based on female specimens of *Brachypotherium aurelianense* (Stehlin 1925 : 113).

*Brachypotherium brachypus*. Stehlin notes that in their morphological characters these supposed *Aceratherium* molars do not differ from those of *Brachypotherium brachypus*, and further that their large size is no valid reason for referring them to *Aceratherium tetradactylum*, which is smaller than *Brachypotherium brachypus*. Moreover, Stehlin notes that in the Pont-Levoy-Thenay deposits there is only one type of lower molar of corresponding size, belonging to *Brachypotherium*. Therefore, the M<sup>2</sup> from Sinda no. 2 should have been referred to *B. heinzellini*. The Congo molar differs from those of *Brachypotherium brachypus* compared in the internal cingulum being weaker (manifested by a large tubercle at the medisinus entrance only), and the crochet being more developed.

There is one specimen of the last upper molar in the Kenya collection that is referable to *Brachypotherium heinzellini*. This is the M<sup>3</sup> dext. from Karungu described and figured but not specifically identified by Andrews (1914: 176-177, pl. 28, fig. 3). The specimen (M. 10632; Pl. 7, fig. 3) is somewhat larger than that of *Aceratherium acutirostratum* from Lake Albert, Congo (Hooijer 1963: 43, pl. 7, figs. 1, 3) in anterior width and the length of the outer surface (Table 13) but has the protocone only weakly constricted off, not by sharp grooves as in *Aceratherium*. It lacks the marked metacone bulge of *Dicerorhinus* from Rusinga in which M<sup>3</sup> is smaller still. The cingulum forms a mere ridge at the medisinus entrance but is otherwise absent internally. The antecrochet is weak, and so is the crochet, while there is a trace of a crista. The upward convergence of parastyle and metastyle as seen from the

TABLE 13

Measurements of upper teeth of *Brachypotherium* (mm.)

|                             | <i>B. brachypus</i><br>M. 33527 | <i>B. heinzellini</i> |                    |         |       |
|-----------------------------|---------------------------------|-----------------------|--------------------|---------|-------|
|                             |                                 | Sinda                 | Rusinga<br>no. 270 | no. 409 | Napak |
| P <sup>3</sup> , ant. post. | 33                              | —                     | 36                 | —       | —     |
| ant. transv.                | 51                              | —                     | 54                 | —       | —     |
| post. transv.               | 52                              | —                     | 54                 | 56      | —     |
| P <sup>4</sup> , ant. post. | 37                              | 49                    | —                  | 48      | —     |
| ant. transv.                | 57                              | 62                    | 61                 | 66      | 64    |
| post. transv.               | 55                              | 58                    | 56                 | 62      | 59    |
|                             |                                 |                       | Karungu            |         |       |
| M <sup>1</sup> , ant. post. | 51                              | —                     | —                  | —       | —     |
| ant. transv.                | 70                              | —                     | 62                 | —       | —     |
| post. transv.               | 60                              | —                     | 52                 | —       | —     |
| p. tr. : a. tr.             | 0.86                            | —                     | 0.84               | —       | —     |
| M <sup>2</sup> , ant. post. | 51                              | 63                    | —                  | —       | —     |
| ant. transv.                | 68                              | 77                    | —                  | —       | —     |
| post. transv.               | 59                              | 63                    | —                  | —       | —     |
| p. tr. : a. tr.             | 0.87                            | 0.82                  | —                  | —       | —     |
| M <sup>3</sup> , ant. post. | 56                              | —                     | 55                 | —       | —     |
| ant. transv.                | 68                              | —                     | 65                 | —       | —     |
| l. outer surface            | 73                              | —                     | 68                 | —       | —     |

external side (Pl. 7, fig. 4) shows the brachyodonty or mesodonty of the crown. The  $M^3$  of *Brachypotherium brachypus* (see Mayet 1909 : 25, text-figs. 11, 12, both from the right side) are indistinguishable from the Karungu specimen but are smaller (antero-transverse diameters 53–59 mm.). The  $M^3$  dext. from Beaugency referred by Mayet (1908 : 98, pl. 3, fig. 6) to *Aceratherium cf. tetradactylum*, but which Stehlin (1925 : 108, footnote 1) states should be referred to *B. brachypus*, is larger (antero-transverse diameter 68 mm.).

The left upper tooth series of *B. brachypus*, the measurements of which are given in Table 13, is from Villefranche d'Astarac (Gers), M. 33527, and is made up of teeth of different individuals (the molar placed as  $M^2$  is more worn than that in the place of  $M^1$ ) but shows the characteristic features of the species. There are external as well as internal cingula in all premolars and molars ; the antecrochet is weak and the protocone constriction slight. The crochet is likewise weakly developed, and the crista is absent except for a trace in  $P^4$ . In the European species, however, the external cingulum may be reduced (Viret 1961 : 69), and so it is in some of the specimens of *B. heinzlini*. In size the African teeth agree rather well with those of *B. brachypus* : the premolars are larger than those of *B. brachypus* presented in the Table, but Viret (1961 : 69) cites a  $P^3$  from La Grive 61 mm. wide, and  $P^4$  68–70 mm. wide, exceeding the large Rusinga specimen no. 409, whereas the Sinda  $M^2$  is larger, the Karungu  $M^1$  and  $M^3$  are however smaller than those in *B. brachypus*. The Sinda  $M^2$  is relatively narrower behind than that in the *B. brachypus* dentition, but the  $M^1$  of that dentition hardly differs from the Karungu  $M^1$  in this respect.

The upper teeth of *Brachypotherium* are larger than those of *Dicerorhinus leakeyi* and *Aceratherium acutirostratum*, and differ further in being relatively narrower behind. Even when the external cingulum is absent the superior size and relatively smaller posterior width are distinctive of *Brachypotherium heinzlini*. The absence of a marked protocone constriction and of a large antecrochet differentiates *Brachypotherium heinzlini* molars from those of *Aceratherium acutirostratum*, while the flattened ectolophs, and the absence of the metacone bulge in  $M^3$  serve to distinguish *Brachypotherium heinzlini* molars from those of *Dicerorhinus leakeyi*.

Although both Osborn (1900 : 250) and Mayet (1908 : 107) state that the external surface of the lower molars of the Burdigalian *B. aurelianense* is flattened, in actual fact this characteristic applies only to the more advanced brachypotheres. Most of the lower molars of *B. aurelianense* have a marked groove on the external surface between metalophid and hypolophid (Stehlin 1925 : 110, 111). In the Upper Burdigalian and Lower Vindobonian *B. stehlini* Viret (1961 : 71), which is generally larger than *B. aurelianense*, the lower molars have the external groove between meta- and hypolophid almost completely flattened out, and moreover almost invariably present an external cingulum (cf. Roman & Viret 1934 : 33, pl. 10, figs. 7, 8). The same characters are found in typical *B. brachypus* of the Upper Vindobonian (Viret 1961 : 72) in which the tendency toward hypsodonty is more marked, as well as in the terminal *B. goldfussi* (Kaup 1834 : 63, pl. 12, figs. 13, 14).

Few lower molars are present in the Rusinga, Karungu, and Napak collections in which the external groove is very shallow or nearly flattened out, and in none of them is

there an external cingulum. These specimens doubtless belong to *Brachypotherium heinzeli*, but whether they are the only ones is not known; some of the grooved specimens may also belong here if this character is not constant in the African species, as happens in *B. aurelianense*. One of the specimens definitely belonging to *Brachypotherium heinzeli*, that from Napak II A, 1964, is rather large, exceeding the *Dicerorhinus leakeyi* lowers in size; the others are not particularly large. The specimens are as follows:

- No. 546, 1949, R. 1, Rusinga, posterior portion of M<sub>1</sub> or M<sub>2</sub> sin. (Pl. 6, fig. 9),  
 No. 345, 1950, Ngira, Karungu, posterior portion of M<sub>1</sub> or M<sub>2</sub> dext.,  
 Napak II A, 1964 (kindly forwarded by Dr. W. W. Bishop), M<sub>2</sub> sin., nearly entire (pl. 8, fig. 2), and  
 M. 25186, R. 7, Rusinga, M<sub>3</sub> sin., incomplete in front.

TABLE 14

Measurements of lower molars of *Brachypotherium heinzeli* (mm.)

|   | Rusinga<br>no. 546  | Karungu<br>no. 345 |
|---|---------------------|--------------------|
| M <sub>1</sub> or M <sub>2</sub> , ant. post. | —                   | —                  |
| ant. transv.                                  | —                   | —                  |
| post. transv.                                 | 29                  | 31                 |
|   | Napak II A          |                    |
| M <sub>2</sub> , ant. post.                   |                     | 56                 |
| ant. transv.                                  |                     | 37                 |
| post. transv.                                 |                     | 35                 |
|   | Rusinga<br>M. 25186 |                    |
| M <sub>3</sub> , ant. post.                   |                     | —                  |
| ant. transv.                                  |                     | 31                 |
| post. transv.                                 |                     | 29                 |

No upper milk molars of *Brachypotherium* appear to be present in the East African Miocene collections. The DM<sup>4</sup> of *Brachypotherium* cf. *brachypus* from Chevilly figured as an M<sup>2</sup> of *Diceratherium douvillei* by Mayet (1908, pl. 3, fig. 5; see Stehlin 1925: 114, footnote) has a stronger cingulum and the protocone less well marked off than the *Aceratherium* DM<sup>4</sup> of Rusinga.

The post-cranial skeleton of *Brachypotherium* is easily distinguished from that of *Dicerorhinus* and *Aceratherium* by the shortness and great relative width of the individual bones. All of the metacarpals are represented in the Rusinga collection:

M. 18813 and M. 18812, Rs. 6a, Rusinga, associated Mc. III and Mc. IV dext.

(Pl. 10, figs. 1, 2). Part of the shaft of the third metacarpal below the magnum facet medially is missing,

F. 3269, R. VII. 1941, Rusinga, Mc. II dext. (Pl. 10, fig. 3), and

M. 18822, Rs. 7, no. 451, 1947, Kathwanga, Rusinga, Mc. IV sin. (Pl. 10, fig. 8).

The median metacarpal is as much shortened as that in the Vindobonian *Brachypotherium brachypus*, whereas the second and fourth metacarpals from Rusinga are

even relatively wider, and more shortened than their homologues in *B. brachypus*, as will be seen by comparing Table 15 with Table 16 (after Roger 1900 : 22).

TABLE 15

Measurements of metacarpals of *Brachypotherium heinzelini* (mm.)

|                              | Mc. II<br>F. 3269 | Mc. III<br>M. 18813 | Mc. IV<br>M. 18812 | Mc. IV<br>M. 18822 |
|------------------------------|-------------------|---------------------|--------------------|--------------------|
| Median length                | 125               | 137                 | 110                | 113                |
| Proximal width               | 52                | 65                  | 45                 | 42                 |
| Proximal ant. post. diameter | 47                | 51                  | 53                 | 46                 |
| Middle width                 | 45                | 53                  | 37                 | 38                 |
| Middle ant. post. diameter   | 25                | 25                  | 24                 | 23                 |
| Greatest distal width        | 50                | 73                  | 52                 | 52                 |
| Width of distal trochlea     | 40                | 59                  | 44                 | 47                 |
| Distal ant. post. diameter   | 38                | 47                  | 39                 | 43                 |

TABLE 16

Measurements of metacarpals of *Brachypotherium brachypus* (mm.)

|               | Mc. II  | Mc. III | Mc. IV  |
|---------------|---------|---------|---------|
| Median length | 100-132 | 130-147 | 116-130 |
| Middle width  | 38-40   | 50-55   | 37-39   |

In *Brachypotherium stehlini* of the Upper Burdigalian of La Romieu the metapodials are longer than those in *B. brachypus* : Mc. II has a median length of 160 mm. by a middle width of 40 mm., and Mc. III has a median length of 170 mm., a proximal width of 70 mm. and the least width of shaft 53 mm. (Roman & Viret 1934 : 33, text-fig. 14, as *B. cf. brachypus* ; cf. Viret 1961 : 71). Thus, as already observed by Stehlin (1925 : 138), the *Brachypotherium* of the Burdigalian has the metapodials less shortened than that of the Vindobonian of La Grive, etc.

Of the *Brachypotherium* from the Miocene of Moghara in Egypt, described as *Teleoceras snowi* Fourtau, no metacarpal, but a left metatarsal III is available. This bone (Fourtau 1920 : 46, text-fig. 30) is longer than that in *B. brachypus*, and in fact is as long as that in *Brachypotherium stehlini* (Roman & Viret 1934 : 33, text-fig. 13A). The ranges of size in *B. brachypus* given in Table 17 are after Roger (1900 : 26) and Viret (1961 : 70).

TABLE 17

Measurements of metatarsal III of *Brachypotherium* (mm.)

|                       | <i>B. snowi</i> | <i>B. stehlini</i> | <i>B. brachypus</i> |         |
|-----------------------|-----------------|--------------------|---------------------|---------|
| Median length         | 151             | 150                | 110-137             | 105-112 |
| Middle width          | c. 50           | 55                 | 45-50               | 47-51   |
| Greatest distal width | 67              | 72                 | up to 70            | 67      |

It follows from this that the Rusinga *B. heinzeli* is more progressive than that of Moghara in Egypt in having more shortened metapodials.

Among the isolated postcranial material from Rusinga there is one entire right radius, M. 18908, Rs. 6a, shorter and wider than the other radii recorded elsewhere in the present paper (Pl. 9, fig. 1). This bone very nearly agrees in dimensions with one of the Steinheim radii recorded by Roger (1900 : 17, table, no. 5) as *Brachypotherium*. The radius of *Brachypotherium stehlini* from La Romieu (Roman & Viret 1934 : 35, pl. 11, fig. 1) has the same proximal and distal widths but is much longer, as seen in Table 18.

TABLE 18  
Measurements of radius in *Brachypotherium* (mm.)

|                       | <i>B. heinzeli</i><br>Rusinga | <i>B. brachypus</i><br>Steinheim | <i>B. stehlini</i><br>La Romieu |
|-----------------------|-------------------------------|----------------------------------|---------------------------------|
| Median length         | 293                           | 300                              | 357                             |
| Proximal width        | 95                            | 98                               | 99                              |
| Middle width          | 52                            | —                                | —                               |
| Greatest distal width | 95                            | 100                              | 101                             |

There are some twenty astragali in the East African Miocene collections, and of these there is one, from the left side, no. 538, Gumba, Rusinga, 1949 (Pl. 14, fig. 3) in which the total width greatly exceeds the medial height, nearly to the same extent as in the astragalus from the type site of *Brachypotherium heinzeli* (Hooijer 1963 : 47, pl. 5, fig. 10 ; pl. 8, fig. 7), and in *B. brachypus* (Table 19). In this Table, the La Grive specimen is after Depéret (1887 : 225, pl. 24, fig. 4), the Steinheim specimen after Roger (1900 : 24), M. 33529 is from Villefranche d'Astarac, and M. 7760 is a cast from Thenay (Loir-et-Cher). The Steinheim astragalus figured by Fraas (1870, pl. 7, fig. 6) is clearly *Brachypotherium* as already surmised by Depéret (1887 : 225), and so is the calcaneum of fig. 9 of Fraas's plate ; both are identified as *Rh. incisivus* by Fraas (1870 : 302).

TABLE 19  
Measurements of astragalus of *Brachypotherium* (mm.)

|                                 | <i>B. heinzeli</i> |         | <i>B. brachypus</i> |           |          |         |
|---------------------------------|--------------------|---------|---------------------|-----------|----------|---------|
|                                 | Sinda              | Rusinga | La Grive            | Steinheim | M. 33529 | M. 7760 |
| Lateral height                  | —                  | 57      | —                   | 73        | —        | —       |
| Medial height                   | 68                 | 60      | 60                  | 68        | 64       | 64      |
| Total width                     | 102                | 82      | 93                  | 96        | 100      | 98      |
| Ratio medial height/total width | 0.67               | 0.73    | 0.64                | 0.71      | 0.64     | 0.65    |
| Trochlea width                  | —                  | 68      | 85                  | —         | 86       | 80      |
| Width distal facets             | —                  | 71      | 85                  | —         | 85       | 85      |

The first phalanx of a median digit, F. 2126, Rusinga, 1941 (Pl. 10, fig. 6), is shorter than any of its homologues in the East African Miocene collections, and more-



over has a proximal width that represents the maximum in our series. The distal articular surface is evenly concave transversely, and flat anteroposteriorly instead of weakly convex as in the longer first phalanges. Its measurements are presented in Table 20; the data on *Brachytherium brachypus* and on *Aceratherium* are after Roger (1900 : 27).

TABLE 20  
Measurements of phalanx I, median digit (mm.)

|                | <i>B. heinzellini</i> | <i>B. brachypus</i> | <i>Aceratherium</i> |
|----------------|-----------------------|---------------------|---------------------|
| Length         | 28                    | 28-30               | 35-45               |
| Proximal width | 55                    | 53-55               | 45-57               |

The second phalanx of a median digit of *Brachytherium heinzellini* is represented by no less than three specimens: F.2125, Rusinga, 1941; M.18854, Rs.101, Rusinga, and M.18862, Rs.6a, Rusinga (Pl. 10, fig. 7). These bones are shorter and wider than their homologues from Rusinga, and their proximal articular surface is evenly convex transversely and flat anteroposteriorly, not raised in the middle in front and behind as in the longer second phalanges. Measurements of *B. brachypus* and *Aceratherium* in Table 21 again after Roger (1900 : 27).

TABLE 21  
Measurements of phalanx II, median digit (mm.)

|                | <i>B. heinzellini</i> |         |         | <i>B. brachypus</i> | <i>Aceratherium</i> |
|----------------|-----------------------|---------|---------|---------------------|---------------------|
|                | F.2125                | M.18854 | M.18862 |                     |                     |
| Length         | 22                    | 20      | 20      | 20                  | 20-35               |
| Proximal width | 58                    | 61      | 59      | 60                  | 40-65               |

The phalanges from Viehhausen provisionally referred to *Brachytherium* cf. *brachypus* by Rinnert (1956 : 37) appear to me to belong to either *Aceratherium* or *Dicerorhinus*.

The first phalanx of a lateral digit, M.18859, Rusinga, is relatively shorter and wider than the others, and agrees with F.2126 in the shape of the distal articular surface. It may therefore be referred to *Brachytherium heinzellini*. The data on *B. brachypus* and *Aceratherium* given by Roger (1900 : 27) are few and apparently questionable; I have added in Table 22 the measurements of some of the first phalanges of lateral digits from Rusinga, including those of the skeleton no. 2 from R.1, Rusinga, 1947.

TABLE 22  
Measurements of phalanx I, lateral digit (mm.)

|                | <i>B. heinzellini</i> | <i>B. brachypus</i> | <i>Aceratherium</i> | Rusinga |    |    |    |
|----------------|-----------------------|---------------------|---------------------|---------|----|----|----|
|                |                       |                     |                     | 37      | 33 | 29 | 28 |
| Length         | 28                    | (20-25)?            | 25-35               | 37      | 33 | 29 | 28 |
| Proximal width | 43                    | (50)?               | 45                  | 40      | 38 | 35 | 40 |

There remains one second phalanx of a lateral digit, no. 1055, S. E. of Kiahera Hill, Rusinga, that is relatively wider than the others, and its proximal surface is evenly convex transversely as in *Brachypotherium*. The data on *B. brachypus* and *Aceratherium* in Table 23 are as given by Roger (1900 : 27); the data on some of the Rusinga second phalanges of lateral digits are added, including those of no. 2, R. 1, 1947.

TABLE 23  
Measurements of phalanx II, lateral digit (mm.)

|                | <i>B. heinzellini</i> | <i>B. brachypus</i> | <i>Aceratherium</i> | Rusinga |    |    |    |    |
|----------------|-----------------------|---------------------|---------------------|---------|----|----|----|----|
| Length         | 22                    | (10-15)?            | 20-30               | 25      | 27 | 25 | 22 | 21 |
| Proximal width | 42                    | (47-50)?            | 45                  | 39      | 37 | 35 | 37 | 27 |

This completes the account of the postcranial material from Rusinga referable to *Brachypotherium heinzellini*. The present species, first described from the Miocene of the Sinda-Mohari region, Lower Semliki, Congo (Hooijer 1963 : 45) on a P<sup>4</sup>, the external cingulum of which has now been shown to be a variable feature, is more advanced than the European *Brachypotherium brachypus* which it resembles dentally, in the lateral metacarpals being more shortened and relatively wider.

Genus **CHILOTHERIUM** Ringström 1924

***Chilotherium*** sp.

(Pl. 6, figs. 10, 11 ; Pl. 7, figs. 1, 2)

An M<sup>3</sup> dext. originating from Loperot 1948 (Pl. 7, figs. 1, 2) represents a genus not before recorded from the African Tertiary. It is well preserved, lacking only a small portion of the internal cingulum at the metaloph, and it is remarkable for two main features, viz., the great height of the crown, and the very weak development of the parastyle fold and the paracone style, characters not seen in *Dicerorhinus*, *Aceratherium*, or *Brachypotherium*.

The external surface of the M<sup>3</sup> (the joined ectoloph and metaloph) is peculiarly flattened and has the sides (parastyle and metastyle) much less converging crownward than in the other genera mentioned : the metastyle is slightly concave basally but becomes very nearly vertical at a level only 15 mm. from the base of the crown, while the parastyle is very steep also. The full basal length of the external surface is 61 mm., which length is reduced to 53 mm. at a height of 15 mm. from the enamel base, and still amounts to 46 mm. at 45 mm. from the base, at which level the crown is worn. Over this vertical distance the thickness of the ectometaloph has hardly reduced, and it is clear that the crown has already undergone a considerable amount of wear. The full height of the unworn crown may well have been some 25 to 35 mm. more than that to which it is worn down, that is, about 70-80 mm. The parastyle fold is hardly visible, and the paracone style is weakly developed in the upper portion

of the crown, flattening out in the basal two-thirds. Near the base, there is a metacone bulge that is, however, placed nearer to the inner end of the external surface than in a *Dicerorhinus* molar. The protocone of the Loperot M<sup>3</sup> is very markedly defined and flattened internally; the anterior and posterior grooves delimiting it become sharper and deeper toward the base, where the posterior groove curves inward to end at the medisinus entrance. The antecrochet becomes very prominent basally, reducing the entrance to the medisinus to a narrow V, while the crochet, which nearly extends all across the medisinus apically, recedes towards the base. There is a weak crista, a projection from the ectoloph opposite the paracone, not yet touched by wear, not reaching the crochet, and like it receding basally. The cingulum is well developed along the anterior surface, absent along the inner surface of the protoloph, forming a cusp entering the medisinus, and continuing along the metaloph, rising to a point 15 mm. high at the metacone bulge posteriorly, beyond which it falls off steeply. There is no cingulum along the external surface.

The great hypsodonty of the Loperot M<sup>3</sup> and the flattening of the external surface as well as the very marked protocone constriction, prominent antecrochet, and metacone bulge near the internal angle, are all characters pointing to its belonging to the genus *Chilotherium* Ringström (1924: 26). This remarkable genus of extinct rhinoceroses with its orbit near the upper surface of the skull, the exaggerated symphysis width and huge, widely separated canines had often been regarded as *Aceratherium* until Ringström (1924) recognized its true character and gave it separate generic status. The specimen from Loperot described above is exceedingly similar in shape and size to the M<sup>3</sup> of *Chilotherium anderssoni* Ringström (1924: 34, 35, pl. 3, figs. 3, 4) from the Pontian of Shansi, North China. The length of the external surface of the M<sup>3</sup> of *C. anderssoni* is 58–60 mm., the anterior width 53–59 mm., and the full height of the crown, presumably the same as in M<sup>2</sup>, about 85 mm. In *C. anderssoni* the metacone bulge is as in the Loperot M<sup>3</sup>; in *C. habereri* (Schlosser) there is no bend at the junction of ecto- and metaloph, the external surface being evenly rounded throughout, and the posterior cingulum is more developed, free at its apex (Ringström 1924: 41, pl. 4, fig. 3). *C. habereri* as well as the other species of *Chilotherium* described from Shansi and Shensi by Ringström are smaller than *C. anderssoni*. In the M<sup>3</sup> of *C. wimani* Ringström (1924, pl. 7, fig. 3) there is a slender crista uniting with the crochet; the internal cingulum is rather variable in the molars but invariably developed at the medisinus entrance.

Table 24 gives the measurements of the Loperot M<sup>3</sup> in conjunction with those of *Dicerorhinus leakeyi*, *Aceratherium acutirostratum*, and *Brachypotherium heinzellini*. While in size the *Chilotherium* M<sup>3</sup> exceeds its homologue in *Dicerorhinus*, it is near to the M<sup>3</sup> of *Aceratherium* and *Brachypotherium* in length, but less wide anteriorly and with the external surface shorter.

In the Rusinga collection there are two incomplete right upper molars that appear to belong to *Chilotherium* as well, viz.,

No. 695, 1949, Gumba, Rusinga, lacking outer portion (Pl. 6, fig. 10), and

No. 506, 1950, Wakondu, Rusinga, protoloph only (Pl. 6, fig. 11).

Both of these show the very markedly constricted and internally flattened proto-

TABLE 24

Measurements of M<sup>3</sup> in various genera (mm.)

|                  | <i>Chilotherium</i> sp.<br>Loperot | <i>Dicerorhinus</i><br><i>leakeyi</i><br>Rusinga | <i>Aceratherium</i><br><i>acutirostratum</i><br>Lake Albert | <i>Brachypotherium</i><br><i>heinzellini</i><br>Karungu |
|------------------|------------------------------------|--|---|---|
| ant. post.       | 56                                 | 42-46  | 57  | 55  |
| ant. transv.     | 60                                 | 50-54  | 62  | 65  |
| l. outer surface | 61                                 | 52-57  | 65  | 68  |

cone, delimited by grooves the posterior of which curves inward basally, the prominent antecrochet, the strongly developed anterior cingulum, and the cingular cusp entering the medisinus: the characters of the Loperot specimen. In the more complete specimen (no. 695) the medisinus is not very well preserved, the molar having been assembled from fragments, but from what is left of the crochet it is evident that it is very prominent, extending forward and outward beyond the antecrochet, as in *Chilotherium*. Moreover, the protoloph (no. 506) is less worn than that in the Loperot M<sup>3</sup>, the internal height of the protocone is 34 mm. Seen from the internal side its crownward taper is less marked than in either *Aceratherium* or *Dicerorhinus* molars, pointing to a high crown.

There does not appear to be any postcranial skeletal material of *Chilotherium* in the East African Miocene collections available to me at present; Ringström (1924) has established that *Chilotherium* is a brachypotherine rhinoceros with the limb and foot bones even more shortened than in *Brachypotherium* (although the metapodials are not so broad at the middle: Ringström 1924: 58, cf. Table 16), and the excellent Rusinga bones here referred to *Brachypotherium heinzellini*.

To the genus *Chilotherium* Ringström refers forms from the Pontian of Samos and of Maragha, Iran, formerly placed in *Aceratherium* (Ringström 1924: 83-89), and the genus occurs also in the Vindobonian of Portugal and Spain (Villalta & Crusafont 1955). The earliest occurrence of the genus in Eurasia is in the Burdigalian Bugti Beds of Baluchistan (whence it was originally described as a hippopotamus: Cooper 1934: 595-596). If the Rusinga and Loperot faunas in which we now have the first evidence of the presence of *Chilotherium* in Africa would be Burdigalian, the appearance of the genus is as early as that in Baluchistan, and earlier than that in Europe.

#### POSTCRANIAL SKELETON OF *Dicerorhinus* AND *Aceratherium*

There is an abundance of postcranial skeletal material in the East African Miocene collections referable to long-limbed rhinoceroses, including much associated or supposedly associated material. Unfortunately, the extensive literature notwithstanding, our knowledge of the skeleton of the Tertiary rhinoceroses of Europe is far from satisfactory, and in particular the distinction between the limb and foot bones of *Dicerorhinus* and *Aceratherium* is well-nigh impossible. In European collections in which these two genera are represented by cranial or dental material, the identifica-

tion of unassociated postcranial material is made mainly on the ground of size, a very uncertain guide. At Steinheim, where both *Dicerorhinus germanicus* Wang and *Aceratherium tetradactylum* (Lartet) (as well as the easily recognizable *Brachypotherium brachypus* (Lartet)) occur, the larger bones have usually been ascribed to *Aceratherium*, the smaller to *Dicerorhinus*, in accord with the size of the teeth in the two slender-limbed forms (Fraas 1870 : 203 ; Roger 1900 : 41 ; Wang 1928 : 203). There is a difference, however slight, between *Dicerorhinus* and *Aceratherium*, for *Aceratherium* is tetradactyl, having a fair-sized metacarpal V, whereas in *Dicerorhinus* the fifth metacarpal is reduced. In the living form of *Dicerorhinus*, *D. sumatrensis* (Fischer), metacarpal V is represented by a rudiment, a sesamoid-like bone that, however, has distinct facets for both metacarpal IV and the unciform. Such rudimentary fifth metacarpals have also been found in the Vindobonian *Dicerorhinus caucasicus* Borissiak (1938 : 38) and in Pleistocene *D. hundsheimensis* (Toula 1902 : 47, pl. 8, figs. 1, 6) ; in both cases the rudiment articulates with unciform as well as with metacarpal IV (Toula describes the fifth metacarpal as " das äussere Sesamknöchelchen "). These mammiform bones are hardly longer than their proximal width. On the other hand, in *Aceratherium tetradactylum* metacarpal V is about 80 mm. long, and has a relatively well-developed distal articulation carrying at least two phalanges, although it is narrow proximally and does not bear proximal facets more extensive than those in *Dicerorhinus*. The fifth metacarpal appears to be developed in all aceratheres, such as *Plesiaceratherium gracile* Young (1937) from Shantung, China, *Aceratherium lemanense* (see Duvernoy 1853, pl. 7, fig. 2, as *A. gannatense* ; Repelin 1917, pl. 12, as "*Teleoceras aginense*" (Lavocat 1951 : 114), and Roman 1924 : 51-52, text-figs. 23, 24), *Aceratherium tetradactylum* (Duvernoy 1853, pl. 7, fig. 1 ; Stehlin 1925 : 132, 139), and the terminal *Aceratherium incisivum* (Kaup 1834 : 58, pl. 15, fig. 4 ; 1854, pl. 9 ; 1859). Stehlin (1917) notes that the *Aceratherium* metacarpal V from Sansan (*A. tetradactylum*) is weaker than that in the earlier *A. lemanense*. Professor H. Tobien (private communication) notes that the two skeletons of *Aceratherium incisivum* of the Pontian of Höwenegg (see Tobien 1956) have a metacarpal V in much the same degree of development as in the Aquitanian *Aceratherium lemanense* as figured by Roman (1924 : 51, text-fig. 23). Detailed studies of the Höwenegg skeletons will yield important data that are, however, not yet available at the time of writing.

Thus, in the absence of an associated metacarpal V, the distinction between the hands of *Dicerorhinus* and *Aceratherium* cannot be made. This does not mean that no attempts have been made to establish distinguishing characters in the postcranial skeleton of the two genera, however, but these do not appear to me to have been successful. They will be referred to as we deal with the skeleton in the pages that follow.

The median metacarpals and metatarsals, considered of the greatest value in rhinoceros taxonomy, are remarkably alike in two (cranially and dentally) well-known species such as *Dicerorhinus sansaniensis* and *Aceratherium tetradactylum* of the Vindobonian of Europe, as is evident from the measurements proffered by Pavlow (1892 : 212) as follows (Table 25) :

TABLE 25

Measurements of median metapodials of *Dicerorhinus* and *Aceratherium* (mm.)

|                                   | Mc. III |       | Mt. III |       |
|-----------------------------------|---------|-------|---------|-------|
|                                   | length  | width | length  | width |
| <i>Dicerorhinus sansaniensis</i>  | 170     | 43    | 150     | 40    |
| <i>Aceratherium tetradactylum</i> | 165     | 42    | 153     | 40    |

There are no significant proportional differences between these bones. It is futile to insist on the value of such minor differences. The great caution exercised by Stehlin (1925 : 125-139) and Arambourg (1933 : 11) in identifying isolated bones of non-brachypothere rhinoceroses is exemplary, and has, I hope, saved me from drawing conclusions not warranted by the evidence.

Among the associated postcranial material of rhinoceroses from the Miocene of East Africa there is first of all that of two skeletons found in 1947 at R. 1, Rusinga. Of these, MacInnes (1951 : 2) writes as follows:

“ The only two complete skeletons yet recovered from the Rusinga deposits have been those of Rhinocerotids. One of these had been exposed on the surface for some considerable time before discovery, and most of the bones were almost weathered away. In the second example, however, the skull, vertebrae, ribs and limbs of the lower side were almost wholly intact and articulated, whilst in the upper half the limbs had been torn off and discarded, though still almost completely articulated, within a few feet of the body. The ribs of the upper side had been forced forwards and backwards from a central point, indicating that the scavengers had penetrated the softer parts of the belly, but had apparently been unable to do any appreciable damage to bones of such bulk. ”

In her book *An outline of the geology of Kenya* Mrs. Sonia Cole published a photograph of the two skeletons *in situ* (Cole 1950, pl. 1), showing one skeleton lying on its side with about twelve ribs arranged neatly in their natural position. This is the most conspicuous feature shown in the picture ; the limb and foot bones lie scattered around although some are in articulation, such as a tibio-fibula and a foot near the centre foreground. The skull (or what remained of it) is not shown in the illustration, and apparently had already been removed before the picture was taken. A scapula with the entire spine and tuber spinae is isolated in the right foreground. The specimen in the picture is from the left side, but in the collection it is from the right side, so that the photograph may have been printed back to front. Whether the thorax was lying with its right side up or with the left side up has not been recorded by MacInnes, but in the published picture the twelve or so ribs, which are those of the lower side (we are looking into the emptied thoracic cavity), are from the left side (the vertebral extremities of the ribs are to the right, and the short and wide first rib is foremost in the picture) ; thus, the right side would have been up before removal from the deposit. In the collection the best-preserved ribs of this skeleton are from the right side, those from the left side preserved being fewer in number and rather fragmentary except for the first and last. This is evidence for the distorted side of the thorax (due to penetration by scavengers) having been the left side, which coro-

borates the conclusion drawn from the scapula that the published photograph has been reversed.

The "de-reversed" picture is given on Pl. 3 of the present paper.

The more complete skeleton of the two from R. 1, Rusinga, 1947, belongs to the upper dentition and mandible of *Dicerorhinus leakeyi* bearing no. 2, R. 1, 1947, although there are a great many bones that are not numbered (the catalogue of the collection sent from the National Museum indicates that all specimens not otherwise marked are thought to belong to skeleton no. 2, R. 1, 1947). In addition, we have the skull remains and mandible marked no. 850 (R. 1), 1947, that represent *Aceratherium acutirostratum*. The skeleton belonging to this skull is the one of which MacInnes writes that it had been exposed on the surface for some considerable time, with most of the bones almost weathered away. Some of the bones of this *Aceratherium* skeleton, viz., the scapula sin., the atlas no. 717, and the left radius and ulna no. 850, are in exactly the same state of preservation as those of the no. 2 *Dicerorhinus* skeleton. These bones are fragmented and distorted, the cracks filled with matrix (or plaster occasionally), whitish in colour and evidently preserved in the broken state in which they had been found. There are a number of bones in a different state of preservation, all much deformed and treated with shellac, which gives a brown staining. These bones, thirteen in all, are invariably from the right side (humerus, radius, ulna, scaphoid, lunar, cuneiform, pisiform, femur, patella, tibia and fibula, astragalus, and calcaneum). It is hardly possible to take measurements of these deformed bones, but the radio-ulna is of the same size as the left numbered 850, slightly smaller than that in *D. leakeyi*, and the shellaced right tibia is also slightly shorter than the homologous bone in the no. 2 skeleton of *Dicerorhinus*. These brownish bones I have no doubt should be regarded as belonging to the no. 850 skeleton of *Aceratherium acutirostratum*; there is no duplication anywhere and the radio-ulnae from both sides agree in size (length). Thus, of the same skeleton we have a few untreated bones from the left side (scapula, radio-ulna) and an atlas, and a great many right bones that have been shellaced.

The picture emerging from these considerations is that of two adult rhinoceros bodies, one (*Dicerorhinus leakeyi*) lying on its right side, the left side of the thorax ripped up by scavengers that tore off some limbs. Of the skull and mandible only the right halves are preserved, the left halves gone. In general, the bones from the right side, more deeply embedded in the sediment, are more complete than the left, although all the larger bones are cracked, distorted and deformed in the course of the fossilization process. The bones of the *Dicerorhinus* skeleton, excluding the smaller elements, are laterally flattened as a result of vertical compression in the fossil deposit. The other body skeleton, slightly smaller and belonging to *Aceratherium acutirostratum*, must have been lying on its left side. The thirteen bones of the right fore and hind limb, still in articulation, had almost weathered away and had to be treated with shellac. The better protected left side of this skeleton, a few bones of which have been saved, could be left untreated.

Here, then, we have two skeletons of different genera, *Dicerorhinus* and *Aceratherium* which would have provided an excellent and rare opportunity to study the

intergeneric postcranial skeletal differences, if any, but the state of preservation of the *Aceratherium* bones and many of the *Dicerorhinus* bones is so poor that they are of no use for detailed morphological comparison. We can only state that the *Aceratherium* individual was slightly smaller than the *Dicerorhinus* individual.

To avoid needless repetition of tables and to facilitate comparison I decided not to describe the *Dicerorhinus leakeyi* skeleton of no. 2 separately under its head, and the *Aceratherium acutirostratum* bones of no. 850 apart (nothing of value can be derived from the latter anyway). Instead, I shall deal with all of the postcranial material of non-brachypothere rhinoceroses, including many specimens of uncertain generic position, in the present work bone for bone. But let us first consider the skeleton as a whole.

The skeleton of *Dicerorhinus leakeyi* from Rusinga, relatively complete as it is, provides a welcome opportunity to compare the lengths of the limb segments in one and the same individual with those in the Recent Sumatran species and in Tertiary species from Europe of which an associated skeleton is known. In the literature we find metrical data on the skeleton of the oldest *Dicerorhinus* species known, viz., the small *D. tagicus* Roman (1924) from the Aquitanian of Budenheim, as well as that of *D. caucasicus* Borissiak (1938) from the Vindobonian Chokrak beds in North Caucasus, the former older, the latter younger than *D. leakeyi*. The data are not so complete as may be desired. The skeleton of *D. leakeyi* lacks the metacarpals, and for the length of this segment I have substituted that of an Mc.IV (M.18814), likewise from R.1, to be dealt with later. Although this bone may be *Aceratherium*, it fits well with the bones of *D. leakeyi*. As this is the only complete metacarpal of a slender-limbed rhinoceros in the collection available from these beds I have used Mc.IV of the other skeletons as well. The radius of the *D. leakeyi* skeleton is incomplete; for the length of this limb segment I have used the length of the ulna from the processus anconaeus. The skeleton of *D. tagicus* does not provide more than approximate lengths of ulna and Mc.IV, but those of the remaining limb segments are accurately recorded. Of the skeleton of *D. caucasicus* the lengths of ulna and Mt.III are not known as these bones are incomplete, and the required lengths of humerus and tibia

TABLE 26

Limb segment lengths and ratios in *Dicerorhinus* (mm.)

|                              | <i>D. tagicus</i> | <i>D. leakeyi</i> | <i>D. caucasicus</i> | <i>D. sumatrensis</i> |
|------------------------------|-------------------|-------------------|----------------------|-----------------------|
| Length of humerus (greatest) | 235               | 450               | c. 400               | 370                   |
| Length of ulna (from beak)   | c. 200            | 400               | —                    | 345                   |
| Length of metacarpal IV      | c. 100            | 150               | 137                  | 130                   |
| Length of femur (greatest)   | 305               | 545               | 450                  | 423                   |
| Length of tibia (greatest)   | 250               | 420               | c. 375               | 313                   |
| Length of metatarsal III     | 122               | 180               | —                    | 144                   |
| Humero-femoral ratio         | 0.77              | 0.83              | c. 0.89              | 0.87                  |
| Ulna-humeral ratio           | c. 0.85           | 0.89              | —                    | 0.93                  |
| Metacarpo-humeral ratio      | c. 0.43           | 0.33              | c. 0.34              | 0.35                  |
| Tibio-femoral ratio          | 0.82              | 0.77              | c. 0.83              | 0.74                  |
| Metatarso-femoral ratio      | 0.40              | 0.33              | —                    | 0.34                  |



are only approximate. However, the available data lead to some interesting conclusions as to the adaptations to speed and weight in the fossil species. The measurements of *D. sumatrensis* are those of an adult male skeleton from Sumatra in the Leiden Museum (cat. ost. g).

The relative lengths of the limb segments shown by the length ratios in Table 26 differ to a greater or less degree in the four skeletons compared. In the skeleton of *D. leakeyi* the hind limb is less elongated relative to the fore limb than in *D. sumatrensis*; the ulna is shorter relative to the humerus, but the tibia longer relative to the femur in the Miocene than in the Recent form. The metapodials of both limbs are very nearly equal in length relative to the proximal limb segments in the two skeletons.

In *D. tagicus*, the oldest (Aquitanian) species, the hind limb is still less elongated relative to the fore limb than in *D. leakeyi*, the ulna again shorter relative to the humerus, the tibia still longer relative to the femur; in all these points the Oligocene skeleton differs more from the Recent than does the Miocene skeleton from Rusinga. But the metapodials, especially of the fore foot, are markedly more elongated relative to the proximal limb segments in *D. tagicus* than in either *D. leakeyi* or *D. sumatrensis*, which differ little in this respect.

The less completely preserved skeleton of *D. caucasicus* shows that the hind limb was probably longer relative to the fore limb than in *D. sumatrensis*; the metacarpohumeral ratio is approximately the same as in *D. leakeyi* and *D. sumatrensis*, while the tibio-femoral ratio is about as in *D. tagicus*.

When years ago I compared the Pleistocene skeleton of *Rhinoceros sondaicus* Desmarest from Java with the Recent skeleton of the Javan rhinoceros I found that the Pleistocene skeleton had radius, tibia, and metapodials longer relative to humerus and femur than the Recent, which I interpreted as evidence of the Pleistocene *Rh. sondaicus* having been a more swiftly-moving type, able to make greater speed, than the Recent. The Pleistocene *Rh. sondaicus* is almost identical in limb segment ratios to Recent *Dicerorhinus sumatrensis*, whereas the Recent *Rh. sondaicus* has the skeletal proportions of the Recent Indian rhinoceros, *Rh. unicornis* L. (Hooijer 1946b). The intraspecific differences in limb segment ratios found in *Rh. sondaicus* are of the same order of magnitude as those now found between *Dicerorhinus leakeyi* and *D. sumatrensis*.

The Aquitanian species *D. tagicus*, with its long manus and pes, represents a definitely more swiftly-moving type than the Miocene and the Recent species. It is interesting to note, however, that *D. tagicus* appears to be fully tridactyl; no facet for Mc. V was found on Mc. IV by Roman (1924: 30). *D. caucasicus*, and probably *D. leakeyi* as well, have a facet for a fifth metacarpal on their Mc. IV, as has the living *D. sumatrensis*. *D. tagicus* is the smallest *Dicerorhinus* known, and has been placed at the beginning of the *Dicerorhinus* "line" (it was unknown to Osborn (1900), who began the line with *D. sansaniensis* of the Vindobonian). The progression into a more slow-moving type along the "line" is shown by the shortened metapodials in the later species. In the relative length of the tibia *D. caucasicus*, although geologically later than *D. leakeyi*, still resembles *D. tagicus*; the long humerus of

*D. caucasicus* appears to exceed even that in the living species, however. It is of course probably fortuitous that *D. leakeyi* should have various limb segment ratios intermediate between those of *D. tagicus* and *D. sumatrensis*, and this gradation should not be regarded as evidence for direct phyletic relationship. However limited the value of the above observations may be, I decided not to leave them out as even the slightest information we can derive from a palaeontological find such as the Rusinga skeleton may be needed later when more comparable Tertiary skeletons in Africa or Europe are discovered.

An atlas (no. 717, Rusinga, 1947, thought to belong to no. 850, R. I, Rusinga, the *Aceratherium acutostratum* skeleton) has incomplete wings, and is crushed from above downwards. The dorsal arch shows the two intervertebral foramina the distance between which is 82 mm. (83.5 mm. in the atlas of *Dicerorhinus primaevus* (Arambourg (1959 : 64) ; 51 mm. in *D. sumatrensis*, Leiden Museum, cat. ost. g). The anterior articular cavities for the occipital condyles are relatively well-preserved, and the width across them is 148 mm. (145 mm. in *D. primaevus*, 139 mm. in *D. schleiermacheri* (Kaup 1834 : 41), and 111 mm. in *D. sumatrensis*). The posterior articular surfaces are damaged, but the median ventral tubercle is entire, 15 mm. long and wide, and 20 mm. high. This tubercle, present in the atlas of *D. schleiermacheri* (Kaup 1834, pl. 13, fig. 1) as well as in that of *D. sumatrensis*, Arambourg (1959 : 64) notes to be almost completely effaced in the specimen of *D. primaevus*.

The scapula is represented by a right and left specimen of the same individual, that of the skeleton of *Dicerorhinus leakeyi* no. 2, R. I, Rusinga, 1947. The spine is broken off in the left, but present and nearly entire in the right scapula ; the tuber spinae is a massive process measuring 75 mm. anteroposteriorly (Pl. 11, fig. 1). The portion of the scapula anterior to the spine (supra-spinous fossa) is not completely preserved in either specimen. The thin anterior border is present in the left ; above the neck portion it is nearly straight. The posterior border of the scapula is concave throughout, and thickened in the middle portion. In the right scapula the posterior angle is missing. The glenoid cavity is incomplete costally in the left specimen. Measurements are given in Table 27 below :

TABLE 27

Measurements of scapula of *Dicerorhinus* and *Aceratherium* (mm.)

|   | <i>Dicerorhinus leakeyi</i> |        | <i>Dicerorhinus sumatrensis</i> | <i>Aceratherium acutirostratum</i> sin. |
|---|-----------------------------|--------|---------------------------------|---|
|   | dext.                       | sin.   |                                 |   |
| Height from anterior border of glenoid cavity to upper end of spine | 495                         | 505    | 355                             | —                                       |
| Ant. post. diameter above tuber spinae                              | —                           | c. 270 | 220                             | —                                       |
| Ant. post. diameter of neck   | 115                         | 115    | 76                              | 110                                     |
| Ant. post. diameter over tuber scapulae and glenoid cavity          | 145                         | 145    | 105                             | 140                                     |
| Ant. post. diameter of glenoid cavity                               | 97                          | 97     | 76                              | 90                                      |
| Transverse diameter of idem   | 78                          | —      | 60                              | 67                                      |
| Transverse diameter of tuber scapulae                               | 61                          | 62     | 32                              | c. 45                                   |

The left scapula of the *Aceratherium acutirostratum* skeleton unfortunately is much less complete, lacking the posterior portion above the neck and most of the spine. The glenoid cavity, however, is distinctly smaller than that in the pair of scapulae of the *Dicerorhinus leakeyi* skeleton from the same site. Further, it may be noted that the tuber scapulae is less extended transversely in the *Aceratherium* than in the *Dicerorhinus* specimens. The measurements have been entered in Table 27.

The proximal portion of a left scapula from Rusinga (M. 18917, marked Rs. 23a) is still less complete; the anteroposterior diameter of the glenoid cavity is 95 mm. Nothing can be said as to its generic position.

In all these scapulae there is a small coracoid process on the costal surface of the tuber scapulae; this process is well developed in a specimen of *Dicerorhinus primaevus* Arambourg (1959: 64) of which no measurements have been given. Of *D. schleiermachi* there is a figure of a scapula (Kaup 1834: 42, pl. 13, fig. 3) with most of the spine missing and incomplete distally. The diameters of the glenoid cavity are given as 79 by 67 mm., smaller than in the specimens of *D. leakeyi*. In *D. sumatrensis* the glenoid cavity is not very much smaller.

Of the humerus we have both the right (Pl. 11, fig. 2) and the left specimen in the skeleton of *Dicerorhinus leakeyi* no. 2, R. 1, 1947. Both are fragmented and crushed to a considerable extent. The right is flattened so that the posterior part of the lateral tuberosity is placed very nearly between the caput and the anterior portion of that tuberosity. Half of the caput and all of the medial tuberosity are gone. The posterior surface is not much damaged proximally, but the deltoid tuberosity is missing and the musculo-spiral groove is flattened. Of the distal half of the right humerus only the lateral condyloid crest and the lateral epicondyle are preserved; the trochlea is missing. The left humerus has most of the trochlea, but the proximal half of the bone is crushed and flattened anteroposteriorly, as are the head and the tuberosities except for the anterior part of the lateral tuberosity, which miraculously escaped damage. Nevertheless, a few measurements can be given, all approximate (Table 28).

A poorly preserved right humerus, shellaced and belonging to the skeleton no. 850 of *Aceratherium acutirostratum*, is too much deformed for measurement.

There are also two humerus portions, the proximal portion of a left specimen (M. 18915) of which the width over caput and lateral tuberosity is only 125 mm., and the distal half of a left specimen (M. 18916) with damaged trochlea and a least shaft width of only 50 mm., greatest distal width 130 mm., of the size of Recent *D. sumatrensis*.

The humerus of *D. schleiermachi* (Kaup 1834: 42, pl. 13, fig. 4) appears to agree rather well with those of *D. leakeyi* (the scapula referred to by Kaup (above) is much smaller). The humerus mentioned by Gaudry (1862-67: 206) to *D. orientalis* is more expanded proximally and distally, and so is that of *D. primaevus* (Arambourg 1959: 66). The proximal width of a specimen of *D. orientalis* measured by Arambourg (1959) is only 154 mm., however. The trochlea width of the humerus of *D. ringstroemi* is 110 mm. (Bohlin 1946: 219).

Of two humeri from Steinheim, Roger (1900: 17) gives measurements entered in Table 28; no. 1 he regards as probably belonging to *Brachypotherium* because of its

TABLE 28

Measurements of humerus of *Dicerorhinus* (mm.)

|   | <i>D. leakeyi</i> |        | <i>D. schleiermachersi</i> | <i>D. orientalis</i> | <i>D. primaevus</i> |
|---|-------------------|--------|----------------------------|----------------------|---------------------|
|   | dext.             | sin.   |                            |                      |                     |
| Greatest length (laterally)                               | —                 | 450    | 457                        | —                    | 442                 |
| Length from caput to medial condyle                       | —                 | c. 390 | —                          | 400                  | 370                 |
| Width over caput and posterior part of lateral tuberosity | c. 150            | —      | 180                        | 190                  | 191                 |
| Width at deltoid tuberosity                               | —                 | 145+   | —                          | 150                  | 156                 |
| Least width of shaft                                      | —                 | c. 75  | 69                         | —                    | 68                  |
| Greatest distal width                                     | —                 | 140+   | 142                        | 160                  | 167                 |
| Width of trochlea   | —                 | c. 110 | —                          | —                    | 110                 |

  

|   | <i>D. sumatrensis</i> | Steinheim |       | La Romieu |
|---|-----------------------|-----------|-------|-----------|
|   |                       | no. 1     | no. 2 |           |
| Greatest length (laterally)                               | 370                   | 420       | 350   | 366       |
| Length from caput to medial condyle                       | 337                   | —         | —     | —         |
| Width over caput and posterior part of lateral tuberosity | 127                   | 140       | 140   | —         |
| Width at deltoid tuberosity                               | 108                   | —         | —     | —         |
| Least width of shaft                                      | 48                    | —         | —     | —         |
| Greatest distal width                                     | 115                   | 155       | 105   | 103       |
| Width of trochlea   | 81                    | 110       | 80    | 77        |

greatest distal width (which exceeds the proximal width); no. 2, which would belong to either *Dicerorhinus* or *Aceratherium*, agrees well in comparative slenderness with the humerus from La Romieu referred to *Aceratherium* cf. *platyodon* Mermier by Roman & Viret (1934: 32, pl. 11, fig. 10).

A left radio-ulna belonging to the skeleton of *Dicerorhinus leakeyi* no. 2, R. 1 (Pl. 11, fig. 3) has the ulna nearly entire but the radius incomplete medially and with the distal end shattered. There is no right radio-ulna of the same skeleton in the Rusinga collection sent to me, but there are a right radius and ulna, shellaced and belonging to the skeleton of *Aceratherium acutirostratum* no. 850, R. 1, 1947, as well as the untreated left radius (Pl. 9, fig. 2) and ulna marked no. 850, which are slightly smaller than the corresponding bones in *D. leakeyi* (Table 29).

Apart from these associated radio-ulnae there are specifically unidentifiable radii and ulnae. There is a right radio-ulna, laterally flattened and restored with plaster, which is marked R. 2 (Rusinga), too badly preserved for measurements to be taken. Then, the proximal part of a right radius (M. 18911, marked Rs. 21, Rusinga) 97 mm. wide, a proximal end of a left (no number discernible) 83 mm. wide, the distal end of a right radius (M. 18910, marked Rs. 31, Rusinga) 78 mm. wide, and three distal ends from the left side, M. 18914, M. 18909, and M. 18912, measuring about 75 mm., 80 mm., and 103 mm. in width, respectively.

TABLE 29  
Measurements of radius and ulna (mm.)

|  | <i>D. leakeyi</i> | <i>A. acuti-<br/>rostratum</i> | <i>D. orien-<br/>talis</i> | <i>D. ring-<br/>stroemi</i> | <i>D. prima-<br/>evus</i> | <i>D. suma-<br/>trens</i> | Steinheim 1         |       |       |
|--|-------------------|--------------------------------|----------------------------|-----------------------------|---------------------------|---------------------------|---------------------|-------|-------|
|  |                   |                                |                            |                             |                           |                           | no. 1               | no. 2 | no. 3 |
| Radius :                                 |                   |                                |                            |                             |                           |                           |                     |       |       |
| Median length                            | 355               | c. 350                         | 330                        | 385                         | 379                       | 293                       | 370                 | 340   | 315   |
| Proximal width                           | 83                | —                              | 70                         | c. 110                      | 105                       | 83                        | 105                 | 87    | 75    |
| Greatest distal w.                       | 90                | —                              | 84                         | 108                         | 102                       | 85                        | 100                 | 90    | 70    |
|  |                   | <i>A. acutirostratum</i>       |                            |                             |                           |                           |                     |       |       |
|  |                   | <i>D. leakeyi</i>              | dext.                      |                             | sin.                      | <i>D. primaevus</i>       | <i>D. sumatrens</i> |       |       |
| Ulna :                                   |                   |                                |                            |                             |                           |                           |                     |       |       |
| Greatest length                          |                   |                                | 440                        | —                           | —                         | 440                       |                     | 396   |       |
| Length from processus anconaeus ("beak") |                   |                                | 400                        | c. 395                      | 395                       | 380                       |                     | 345   |       |
| Length of olecranon (from "beak")        |                   |                                | 160                        | 155                         | —                         | 145                       |                     | 125   |       |
| Width at semilunar notch                 |                   |                                | —                          | —                           | 73                        | —                         |                     | 69    |       |
| Middle width                             |                   |                                | —                          | —                           | 45                        | 45                        |                     | 39    |       |
| Greatest distal diameter                 |                   |                                | 67                         | —                           | —                         | 67                        |                     | 56    |       |

The radius of *D. orientalis* (Gaudry 1862-67 : 206, pl. 32, fig. 4) is somewhat more slender than that of *D. leakeyi* distally ; that of *D. ringstroemi* (Ringström 1924 : 15 ; Bohlin 1946 : 221) on the other hand is wider distally and agrees rather well with the average of five radii of *D. primaevus* given by Arambourg (1959 : 67). The ulna of *D. primaevus* does not differ much in size from those of *Dicerorhinus* and *Aceratherium* from Rusinga, but in one of the *primaevus* ulnae (no. 197) the olecranon is rather short (88 mm.?).

Eight radii from Steinheim (Roger 1900 : 17) vary in length from 295 to 370 mm. and in distal width from 65 to 100 mm. Those with the greatest distal width (100 mm.) Roger regards as probably referable to *Brachypotherium*, but the specimens that have this distal width range in length from 300 to 370 mm. That of which the length is 300 mm. (no. 5 in Roger's table) agrees well with a Rusinga radius that I refer in the present paper to *Brachypotherium heinzellini* (Table 18). The measurements of the largest three Steinheim radii of Roger's are given in Table 29 ; Roger would refer only no. 3 to either *Dicerorhinus* or *Aceratherium*, but nos. 1 and 2 do not differ much in dimensions from those in various fossil *Dicerorhinus* species and may belong to this genus or to *Aceratherium*.

Of the skeleton of *Aceratherium acutirostratum* no. 850, R. 1, 1947, we have the three proximal carpals, scaphoid, lunar and cuneiform (Pl. 14, figs. 4, 5) as well as the pisiform from the right side ; these bones were evidently in articulation in the deposit and are much deformed as a whole, fitting well on to each other but inadequate for accurate measurement.

There are three isolated left scaphoids, one from Karungu (M. 18897) (Pl. 14, fig. 6), and two marked KB.A, Maboko (= Kiboko) Island (M. 18896 and M. 18898), and also the anterior portion of a left specimen (M. 18899). These bones are similar in proportions and differ only in size; the smallest is even exceeded in size by the scaphoid in *D. sumatrensis* (Table 30).

TABLE 30  
Measurements of scaphoid (mm.)

|                      | M. 18897 | M. 18898 | M. 18896 | M. 18899 | <i>D. sumatrensis</i> |
|----------------------|----------|----------|----------|----------|-----------------------|
| Posterior height     | 71       | 65       | 50       | —        | 56                    |
| Anterior height      | 55       | 49       | 41       | 55       | 55                    |
| Proximal width       | 49       | 44       | 38       | —        | 47                    |
| Distal width         | 47       | 41       | 37       | —        | 47                    |
| Ant. post. at middle | 66       | 58       | 51       | —        | 65                    |

The Karungu and Maboko Island bones resemble that of *D. schleiermacheri* (Kaup 1834 : 43, pl. 13, fig. 9) in shape except that their posterior height is relatively greater. The proximal projection behind the saddle-shaped radius facet and the distal projection behind the trapezium facet are more developed than in the Eppelsheim specimen, and the height taken over these projections greatly exceeds the height taken in front, over the convexity of the radius facet and the ridge between the facets for trapezium and magnum. Kaup gives neither of these measurements in the text, but from his figures it is clear that the posterior height in *D. schleiermacheri* is only slightly the greater, and so it is in *D. sumatrensis*. Kaup does give the length of the three distal facets (for trapezium, trapezoid, and magnum) as 61 mm., and that of the proximal facets as 49 mm.; these figures agree closely with those in the largest of our scaphoids. The total length of the Eppelsheim bone is given as 90 mm.; the greatest diameter of the Karungu scaphoid, measured over the posterior upper end and the distal outward projection is slightly less (86 mm.). This projection does not extend outward beyond the radius facet, and thus the distal width does not exceed the proximal width, as it does in *Brachypotherium* in contradistinction to *Aceratherium* (and *Dicerorhinus*) (Roger 1900 : 19). The scaphoid of *D. ringstroemi* (Ringström 1924 : 15, fig. 6; Bohlin 1946 : 222, text-fig. 78-2) is much larger than any of our specimens: the greatest diameter is 104 mm., the anterior height 69 mm., although the width of the proximal facet is only 47 mm. Arambourg (1959 : 67) gives measurements of the scaphoid of *D. primaevus*, viz., maximal height 55 mm., and "longueur maxima" (evidently anteroposteriorly) 61 mm., which makes the bone intermediate in size between M. 18897 and M. 18898. The deformed scaphoid of the proximal carpal series of *Aceratherium acutirostratum* (no. 850) is approximately 55 mm. high anteriorly.

One lunar, marked Rs., Rusinga (M. 18906), is from the right side and incomplete behind; another, marked R. 2, Rusinga (M. 18907), from the left side and incomplete medially. Both have a proximal lateral facet for the ulna, as in *Aceratherium* and *Dicerorhinus*, although in M. 18906 it is very small. The last-mentioned specimen

(Table 31) closely agrees with the lunar of *D. sumatrensis* in shape as well as size. The anterior height of M. 18907 is greater, as in a lunar from Steinheim referred to *Aceratherium* by Roger (1900 : 19). The bone in question of *D. schleiermacheri* is figured only by Kaup (1854, pl. 7); that of *D. ringstroemi* is figured by Bohlin (1946 : 223, text-fig. 79-2), with measurements, while that of *D. primaevus* (Arambourg 1959 : 67) is unfigured. The deformed lunar in the associated proximal carpal series of no. 850 (*Aceratherium acutirostratum*) is about 55 mm. high and wide.

TABLE 31  
Measurements of lunar (mm.)

|                              | M. 18906 | M. 18907 | <i>D. ringstroemi</i> | <i>D. primaevus</i> | <i>D. sumatrensis</i> | Steinheim |
|------------------------------|----------|----------|-----------------------|---------------------|-----------------------|-----------|
| Anterior height              | 40       | 47       | 61                    | —                   | 40                    | 48        |
| Proximal width               | 45       | —        | 62                    | 50                  | 44                    | —         |
| Greatest ant. post. diameter | —        | 68       | 77                    | 67                  | 65                    | 64        |

A right cuneiform from Karungu (M. 18903), and a left from Rusinga (M. 18904), the latter damaged anteriorly below, are rather small, smaller than that in *D. sumatrensis*, but closely similar to it. A left cuneiform from Rusinga (M. 25184) is incomplete externally below, and slightly larger. This bone in *D. primaevus* (Arambourg 1959 : 67, "Pyramidal") is rather extended horizontally. The cuneiform of *Aceratherium acutirostratum* (no. 850) has an anterior height of about 48 mm.

TABLE 32  
Measurements of cuneiform (mm.)

|                              | M. 18903 | M. 18904 | M. 25184 | <i>D. primaevus</i> | <i>D. sumatrensis</i> |
|------------------------------|----------|----------|----------|---------------------|-----------------------|
| Anterior height              | 38       | —        | 50       | 46                  | 46                    |
| Distal width                 | 32       | 33       | —        | —                   | 38                    |
| Proximal ant. post. diameter | 25       | 26       | 32       | —                   | 29                    |
| Greatest horizontal diameter | 36       | —        | —        | 50                  | 48                    |

The pisiform is available only in the deformed right carpal series. It is over 60 mm. in length, and at least 40 mm. in distal height (50 mm., and 33 mm. in *D. sumatrensis*). The proximal facets are injured, but one fits well on to the cuneiform.

A right magnum, marked Rs. 101, Rusinga (M. 18902) is incomplete anteriorly and medially and lacks most of the posterior downward process. A right and a left magnum marked R. 3, Rusinga (M. 18900 and M. 18901), however, are well preserved. The posterior process is much more developed transversely in the right than in the left specimen, *D. sumatrensis* being intermediate in this respect (Table 33); *D. primaevus* is unfigured.

Two well-preserved unciforms, one right, marked Rs. 31, Rusinga (M. 18884), and one left, Kathwanga, Rusinga (M. 25191) (Pl. 14, fig. 7) resemble that in *D. sumatrensis*

TABLE 33  
Measurements of magnum (mm.)

|                              | M. 18902 | M. 18900 | M. 18901 | <i>D. primaevus</i> | <i>D. sumatrensis</i> |
|------------------------------|----------|----------|----------|---------------------|-----------------------|
| Greatest anterior height     | c. 33    | 25       | 27       | 33                  | 30                    |
| Greatest anterior width      | —        | 38       | 36       | 39                  | 42                    |
| Proximal ant. post. diameter | 65       | 53       | 57       | —                   | 67                    |
| Greatest diameter            | —        | 82       | 75       | 85.5                | 79                    |

very well indeed. The unciform of *D. schleiermacheri* (Kaup 1834 : 43, pl. 13, fig. 8) is rather small, apparently of a young individual; those of *D. ringstroemi* (after Bohlin 1946 : 225) present dimensions greater than the Rusinga specimens (Table 34).

TABLE 34  
Measurements of unciform (mm.)

|                              | M. 18884 | M. 25191 | <i>D. schleiermacheri</i> | <i>D. ringstroemi</i> | <i>D. sumatrensis</i> |
|------------------------------|----------|----------|---------------------------|-----------------------|-----------------------|
| Greatest anterior height     | 45       | 51       | —                         | —                     | 49                    |
| Greatest width               | 60       | 68       | 54                        | c. 74 78              | 61                    |
| Greatest ant. post. diameter | 80       | 94       | —                         | 105 108               | 77                    |

In the Rusinga collection there is an entire Mc.IV sin., M. 18814, marked R. 1, Rusinga, that is associated with the proximal portion of an Mc.III sin., M. 18841, with the same inscription. That these bones belong to the same individual cannot be doubted; their state of preservation is exactly the same and there could not be a better fit (Pl. 12, figs. 2, 3). Then there is the proximal portion of an Mc.II sin. (M. 18843) that would seem to belong to the same individual but that is marked Rs., which means that it is a specimen picked up from the surface and not found *in situ* (cf. Le Gros Clark & Leakey 1951 : 3). Its preservation is exactly that of the Mc. III-IV, and size and proximal articulation with Mc. III could not be more fitting.

There is another set of metacarpals from Rusinga representing one or two individuals, and again from the left side. Here are the proximal portions only, that of Mc.II (M. 18842) marked Rs. (surface find), but those of Mc.III (M. 18837) and Mc.IV (M. 18840) marked Rs. 31 (Pl. 12, fig. 4). These bones are all incomplete behind, Mc.IV laterally too, and smaller than the set first mentioned.

In both Mc.IV (M. 18814 and M. 18840) there is a small lateral proximal facet, placed anteriorly, making an obtuse angle with the large proximal unciform facet and only 6-8 mm. wide by an anteroposterior diameter of some 20 mm. There is no posterior-interproximal facet on the lateral side of Mc.IV. Now this facet articulated with Mc.IV, but whether this was a mere rudiment or a sizable though small metacarpal it is impossible to tell. As related above (p. 153) *Dicerorhinus* so far as known has a mammiform Mc.V as extended proximally as the short Mc.V in *Aceratherium*,



giving the same small facets for articulation with its neighbour and with the unciform (cf. Kaup 1859). Only the find of an Mc. V, associated, would tell the genus to which the other metacarpals belong. Hence, it is uncertain whether the two sets of metacarpals belong to *Dicerorhinus* or to *Aceratherium*, and we have to leave it at that.

Without mentioning these facets, Roger (1900 : 41) writes that the proximal (unciform) facet of Mc. IV in *Aceratherium* is distinctly wider in front, and more rapidly reduces in width posteriorly than that in *Dicerorhinus*, which has a relatively narrower and more anteroposteriorly elongated unciform facet. However, the unciform facet in Recent *D. sumatrensis* Mc. IV is shaped exactly as that in the Rusinga Mc. IV, and of *Aceratherium* I have no reliable material for comparison. The character mentioned as distinctive of the fourth metatarsal of *Aceratherium* by Roger (1900) is found in that of *Dicerorhinus leakeyi* and will be mentioned later on. It seems best to leave the generic position of the metacarpal sets in doubt, although Mc. IV of the larger set fits well with the other bones of *D. leakeyi* as can be seen in Table 26.

There is further an isolated Mc. IV, from the right side (M. 18811, Rusinga), that lacks the posterior proximal portion but permits of the median length to be taken (Pl. 12, fig. 1) ; it is more slender than M. 18814 but less so than M. 18840, and its measurements have likewise been included in Table 35.

The metacarpals of *D. schleiermachi* are an Mc. III sin. and an Mc. II sin., the latter erroneously described as a right outer (fourth) metacarpal (Kaup 1834 : 43, pl. 13, figs. 13 and 12 ; 1854, pl. 7). The greatest length of Mc. III is given as 204 mm., that of Mc. II as 178 mm. (200 mm., and 177 mm., in Kaup 1854). The median length of the median metacarpal of *D. schleiermachi* would be some 190-194 mm., 10 mm. less than the greatest length, at any rate exceeding that of *D. primaevus* as given by Arambourg (1959 : 68). The Mc. III of *D. orientalis* (Gaudry 1862-67 : 205/6, pl. 32, fig. 6) has a median length of 164 mm. and a greatest distal width of 61 mm. Of *D. ringstroemi* the left metacarpals III and IV have been made known by Ringström (1924 : 15, fig. 10). The Mc. III has a median length of 187 mm., and a greatest distal width of 68 mm. (even 73 mm. in an incomplete Mc. III). The Mc. IV of *D. ringstroemi* has a median length of 153 mm. and a greatest distal width of 50 mm., measurements that agree very well with those of M. 18814. Of *D. primaevus* measurements have been entered in Table 35 ; Mc. IV is shorter and less expanded distally than that of *D. ringstroemi* and the Rusinga specimen, while Mc. III of *D. primaevus* is likewise shorter and less wide distally than that of *D. ringstroemi*. The longest metacarpals are those of *D. schleiermachi*, and its fourth metacarpal, when known, would probably exceed that of *Dicerorhinus leakeyi* in size. In *D. primaevus* Mc. IV is slightly more shortened relative to Mc. III than in *D. sumatrensis*. It will be observed that the metacarpals of the living species are relatively more expanded distally than those in the Rusinga *Dicerorhinus* or *Aceratherium*. The relative width of the fourth metacarpal in *D. sumatrensis*, however, is exactly the same as that in the Rusinga form.

An Mc. III from Steinheim referred to *Aceratherium* by Roger (1900 : 40) is as long as that of *D. schleiermachi* : its length is 192 mm. and the middle width 55 mm.

TABLE 35  
Measurements of metacarpals (mm.)

|                              | M. 18843 | M. 18842 | <i>D. primaevus</i> | <i>D. sumatrensis</i> |
|------------------------------|----------|----------|---------------------|-----------------------|
| Mc. II                       |          |          |                     |                       |
| Median length                | —        | —        | 156                 | 136                   |
| Proximal width               | 43       | 39       | —                   | 35                    |
| Proximal ant. post. diameter | c. 47    | —        | —                   | 37                    |
| Middle width                 | c. 38    | c. 33    | —                   | 34                    |
| Middle ant. post. diameter   | —        | —        | —                   | 18                    |
| Greatest distal width        | —        | —        | 41                  | 47                    |
| Width of distal trochlea     | —        | —        | —                   | 36                    |
| Distal ant. post. diameter   | —        | —        | —                   | 41                    |
| Mc. III                      | M. 18841 | M. 18837 |                     |                       |
| Median length                | —        | —        | 179                 | 158                   |
| Proximal width               | 64       | 49       | —                   | 57                    |
| Proximal ant. post. diameter | 55       | c. 40    | —                   | 47                    |
| Middle width                 | c. 50    | 42       | —                   | 45                    |
| Middle ant. post. diameter   | —        | 18       | —                   | 18                    |
| Greatest distal width        | —        | —        | 61                  | 59                    |
| Width of distal trochlea     | —        | —        | —                   | 48                    |
| Distal ant. post. diameter   | —        | —        | —                   | 42                    |
| Mc. IV                       | M. 18814 | M. 18811 |                     |                       |
| Median length                | 150      | 145      | 140                 | 130                   |
| Proximal width               | 51       | 41       | —                   | 42                    |
| Proximal ant. post. diameter | 47       | —        | —                   | 42                    |
| Middle width                 | 34       | 34       | —                   | 30                    |
| Middle ant. post. diameter   | 21       | 21       | —                   | 17                    |
| Greatest distal width        | 50       | 44       | 38                  | 45                    |
| Width of distal trochlea     | 44       | 40       | —                   | 38                    |
| Distal ant. post. diameter   | 41       | 37       | —                   | 41                    |
| Ratio middle width/length    | 0.23     | 0.23     | —                   | 0.23                  |

Three Steinheim Mc. IV referred to *Aceratherium* by the same author are 150–160 mm. in length, and 30–31 mm. in middle width, very slightly more slender in the shaft than the Rusinga form.

TABLE 36  
Measurements of metacarpals (mm.)

|                              | M. 18845 | M. 18848 | K. 4,<br>1950 | M. 18838 | M. 18839 | M. 18851 | M. 25183 |
|------------------------------|----------|----------|---------------|----------|----------|----------|----------|
| Proximal width               | 41       | 39       | 41            | 55       | 58       | 53       | 48       |
| Proximal ant. post. diameter | —        | —        | —             | 42       | 50       | 46       | 45       |

In addition to the above-mentioned metacarpals there are various proximal metacarpal portions that belong either to *Dicerorhinus* or to *Aceratherium*, viz., M. 18845, Rusinga, Mc. II sin., damaged behind, M. 18848, Kachuku, Lower Series, Karungu, Mc. II dext., incomplete behind, K. 4, 1950, Ngira, Karungu, Mc. II sin., articular surface incomplete,

- M. 18838, Rusinga, Mc. III dext.,  
 M. 18839, Rs. 103, Rusinga, Mc. III dext.,  
 M. 18851, Kachuku, Lower Series, Karungu, Mc. III sin., and  
 M. 25183, Rusinga, Mc. III sin.

Four phalanges are unnumbered and associated ; they are thought to belong to the skeleton of *Dicerorhinus leakeyi* no. 2, R. 1, 1947. They comprise the first and second phalanges of the median digit and of a lateral digit, and if they belong to the no. 2 skeleton they form part of the fore foot as the median phalanges of both hind feet of the skeleton are present. Measurements are given in Table 37.

TABLE 37  
 Measurements of anterior phalanges (mm.)

|                    | Rusinga      |               | <i>D. primaevus</i> |               | <i>D. sumatrensis</i> |     |    |
|--------------------|--------------|---------------|---------------------|---------------|-----------------------|-----|----|
|                    | median digit | lateral digit | median digit        | lateral digit | II                    | III | IV |
| Phalanx I, length  | 36           | 37            | 39                  | 42            | 34                    | 33  | 31 |
| Proximal width     | 50           | c. 41         | 55                  | 39.5          | 39                    | 48  | 40 |
| Phalanx II, length | 26           | 25            | 27                  | 28            | 23                    | 26  | 23 |
| Proximal width     | 53           | 39            | 55                  | 40            | 34                    | 52  | 35 |

There is a considerable number of fragments of ribs, some annotated, some not, all belonging to the skeleton of *Dicerorhinus leakeyi* no. 2, R. 1, 1947. Encouraged by the photograph published by Cole (1950, pl. 1), which shows that at least the ribs of one side had been mostly there in a complete state, I have tried to reassemble the fragments, and arrange them, after determining the side to which the ribs belong (possible in most cases), in such a way as to obtain a graded series. The head and tubercle, the relative size and position of which gradually change as one passes along the series, are only rarely available, but using Recent rhinoceros skeletons of various genera (*Diceros*, *Rhinoceros*, and *Dicerorhinus*) in the Leiden Museum as a guide, it has been possible to determine all but a few of the twenty right ribs that were on the lower side of the skeleton before excavation, and about half that number of left ribs. The numbering of the fossil ribs is, of course, to some extent provisional.

To begin with, the ribs, and especially the wide anterior ribs up to about the ninth, are distorted, as are most of the larger bones of this skeleton. In some of the ribs, when laid with their posterior border on a table, the body does not stand up but is nearly flat on the table. The sternal ends are better preserved than the vertebral.

The first rib, easily recognizable because of its large tubercle, shortness, and rapid increase in greatest diameter toward the sternal end, is present from both sides. The left rib is best preserved, the head only being lost. The lateral flattening and distortion (there is a peculiar S-twist near the middle of the body that is unnatural) are severe, however. Its greatest length is 280 mm., the maximal diameter at the sternal end 50 mm., while at the narrowest point below the (missing) head it measures 28 mm. anteroposteriorly and 17 mm. transversely in cross section. In the right first rib both extremities have been lost ; the cross section as taken on the left rib is 22 by

20 mm., showing that the right rib is less laterally compressed than the left. In an adult male of *D. sumatrensis* used for comparison with the fossil skeleton throughout the first rib is 230 mm. long, 33 mm. in greatest sternal diameter, and 20 by 13 mm. in section below the head.

The second rib, from the right side, is a slightly curved specimen without head or tubercle but with the sternal end. Length as preserved 380 mm. (the length of the complete second rib in *D. sumatrensis*), and greatest diameter at middle of body 40 mm. (24 mm. in *D. sumatrensis*). Of the left second rib the proximal portion only is present in the collection.

The head and tubercle are preserved in the anterior of two right ribs that are still held together by matrix proximally. They agree best with the third rib in Recent skeletons in the configuration of the vertebral end. The third rib, then, is incomplete sternally; length 490 + mm. (440 mm. in *D. sumatrensis*), and greatest diameter at middle 36 mm. (26 mm.). The fourth right rib, the sternal end of which is preserved, had a length of about 600 mm. (520 mm.) when complete, by a greatest diameter at middle of about 50 mm. (29 mm.).

The (?) fifth right rib lacks a portion of the body that I have been unable to find among the fragments; diameter at middle of about 50 mm. (32 mm.). The (?) sixth right rib which has the sternal end but no head, is 530 mm. long as preserved, and 52 mm. (30 mm.) in greatest middle diameter. The (?) seventh right rib is without the vertebral end, a body fragment only 275 mm. long and 49 mm. in greater diameter.

What is probably the sixth or seventh left rib is an entire specimen, 750 mm. long along the curve, and 50 mm. in diameter along most of its length. In *D. sumatrensis* the sixth and seventh ribs are 630–670 mm. long and 27–30 mm. in diameter.

The (?) eighth right rib is entire, with a length of 900 mm. (700 mm.) and a greatest diameter of 42 mm. (22 mm.).

A number of right ribs, all without the vertebral end, have the same curvature as the (?) eighth, and either the same or a smaller thickness. These I have arranged so that the sternal end decreases in size posteriorly. The best preserved is the (?) eleventh rib, of which the costal tubercle at least (already much reduced) is present. The total length is probably 900 mm. (730 mm.) and the greatest diameter 34 mm. (23 mm.).

From the eleventh rib onwards the ribs in Recent species become very thin medio-laterally (least so in *Rhinoceros*), whereas the fossil ribs assigned to this region are more robust. The curvature remains the same until the seventeenth rib has been reached. We have the greater part of what appear to be the twelfth to seventeenth ribs from the right side, and fragments of the ninth to thirteenth ribs from the left side, the side into which the scavengers penetrated. The greatest diameters of the incomplete specimens vary from 30 to 37 mm. (21–26 mm. in *D. sumatrensis*). The almost entirely preserved (?) eleventh rib must have been one of the longest, as in the Recent species the length starts to decrease backward from about the eleventh rib.

The penultimate and last ribs are very thin at their free end, which are preserved in what appear to be the eighteenth, nineteenth, and twentieth ribs from the right side. But the last rib (twentieth?) from the left side even has the vertebral end too,

in which tubercle and head have become united. Its length along the curve is 410 mm., the greatest vertebral diameter 39 mm., at the free end 10 mm. In *D. sumatrensis* the twentieth rib is absent although the nineteenth is still 420 mm. long. In *Diceros bicornis* (L.) one skeleton (Leiden Museum reg. no. 5738) has the twentieth and last rib with the same diameters at the ends as in the fossil, but its length is only 280 mm.

Of the pelvis of the skeleton of *Dicerorhinus leakeyi* no. 2, R. 1, 1947, there is only a portion from the right side, which shows the acetabulum, part of the shaft of the ilium, and the pubis and ischium around the obturator foramen, but the specimen is fragmented and distorted to such a degree that no measurements can be recorded.

The left femur is one of the best preserved bones of the skeleton of *D. leakeyi* no. 2, R. 1, 1947. Its distal part is slightly displaced relative to the proximal portion, but the usual flattening is not extensive (Pl. 13, fig. 1). The right femur of the same individual has the distal end crushed and incomplete, and the proximal end missing. It has, however, the (flattened) third trochanter, broken off in the left specimen. Measurements are recorded in Table 38.

TABLE 38  
Measurements of femur of *Dicerorhinus* and *Aceratherium* (mm.)

|  | <i>D. leakeyi</i><br>sin. | <i>D. schleier-</i><br><i>macheri</i> | <i>D. orientalis</i> (Pikermi) |             |       |        | <i>D. ring-</i><br><i>stroemi</i>       | <i>D. prima-</i><br><i>evus</i> |
|--|---------------------------|---------------------------------------|--------------------------------|-------------|-------|--------|---|---------------------------------|
|  |                           |                                       | (Gaudry)                       | (Arambourg) |       |        |   |                                 |
| Greatest length                            | 545                       | 555                                   | 540                            | 491         | 499   | —      | 538                                     |                                 |
| Proximal width                             | 215                       | —                                     | —                              | 192         | 198   | —      | 223                                     |                                 |
| Least width of shaft                       | 75                        | —                                     | 90                             | 75          | 75    | —      | 82                                      |                                 |
| Greatest distal width                      | c. 145                    | 153                                   | 155                            | 145         | 146   | 170    | 150                                     |                                 |
| Distal ant. post.<br>diameter, medial side | 180                       | 160                                   | —                              | —           | —     | c. 235 | —                                       |                                 |
| Transverse diameter<br>caput               | 95                        | —                                     | —                              | —           | —     | —      | —                                       |                                 |
|  |                           |                                       | Steinheim (Roger 1900)         |             |       |        |   |                                 |
|  |                           | <i>D. sumatrensis</i>                 | no. 1                          | no. 2       | no. 3 | no. 5  | <i>Aceratherium</i><br><i>incisivum</i> |                                 |
| Greatest length                            |                           | 423                                   | 540                            | 533         | 450   | 395    | —                                       |                                 |
| Proximal width                             |                           | 162                                   | —                              | —           | —     | —      | —                                       |                                 |
| Least width of shaft                       |                           | 56                                    | —                              | —           | —     | —      | —                                       |                                 |
| Greatest distal width                      |                           | 125                                   | 150                            | 138         | 110   | 105    | 123                                     |                                 |
| Distal ant. post. diameter,<br>medial side |                           | 150                                   | —                              | —           | —     | —      | 149                                     |                                 |
| Transverse diameter caput                  |                           | 73                                    | —                              | —           | —     | —      | —                                       |                                 |

The right, shellaced femur of the skeleton of *Aceratherium acutirostratum* no. 850, R. 1, 1947, consists of the proximal and distal portions that do not fit, and the deformation does not permit of measurements to be taken. There is also the isolated caput of a femur, no. 991, Rusinga, 1947, that measures 79 mm. transversely, almost as small as in *D. sumatrensis*.

The femur of *D. leakeyi* agrees very well in size with the largest femur of *D. primaevus* (Arambourg 1959 : 70) given in the Table ; that of *D. schleiermacheri* (Kaup 1834 : 44, pl. 13, fig. 5) is longer than either of them. The femur of the Pikermi *D. orientalis* as given by Gaudry (1862-67, pl. 32, fig. 7) is rather similar, but the femora recorded by Arambourg (1959 : 70) as belonging to the same species are noticeably shorter. The bone in *D. ringstroemi* (Bohlin 1946 : 227) is wider distally than any of the others presented in Table 38. Of the Steinheim femora recorded by Roger (1900 : 17) the largest (no. 1) is like that of *D. leakeyi* in the few measurements given. Roger would refer most of the Steinheim femora to *Brachypotherium* except the slender (and short) no. 5, which he would place with *Aceratherium*. The femur referred to *Aceratherium incisivum* by Kaup (1834 : 59, pl. 15, fig. 1) has a greater distal width than Roger's nos. 3 and 5, but its length is unknown. The *Aceratherium* (or *Dicerorhinus*?) femur agrees with that of *D. sumatrensis* in size.

The patella is represented by five specimens. No. 718, which belongs to the skeleton of *Dicerorhinus leakeyi* no. 2, R. 1, 1947, is corroded, rather small, and drawn out in a point distally. There are a large right specimen belonging to the skeleton of *Aceratherium acutirostratum* no. 850, distorted and incomplete, and three unnumbered specimens, one left and two right, the last of which bears the mark Rs. 31, Rusinga.

TABLE 39  
Measurements of patella (mm.)

|        | <i>D. leakeyi</i><br>dext. | <i>A. acuti-<br/>rostratum</i> | sin. | dext. | dext.<br>Rs. 31 | <i>D. sumatrensis</i> |
|--------|----------------------------|--------------------------------|------|-------|-----------------|-----------------------|
| Length | 76+                        | —                              | 84   | 98    | 105             | 91                    |
| Width  | 60+                        | 85                             | 83   | 87    | 82              | 77                    |

It may seem peculiar that the patella of the *Dicerorhinus* from Rusinga (it fits well on to the articular surface of the right femur, and certainly belongs to the no. 2 skeleton) is so much smaller than that of the *Aceratherium*, whereas in the other bones of the two skeletons *D. leakeyi* is (slightly) the larger as far as can be seen. The patella, however, may be just abnormally stunted in the *D. leakeyi* skeleton ; it is unfortunate that we do not have this bone from the left limb also.

The patella of *D. schleiermacheri* (Kaup 1834 : 44, pl. 13, fig. 7) differs from that referred to *Aceratherium incisivum* (Kaup 1834 : 60, pl. 15, fig. 12) in being more squarish ; that of *A. incisivum* (it should be noted that it has been figured upside down) is more drawn out medially. The length is 90 mm. in both ; the width about 80 mm. in *D. schleiermacheri* against 94 mm. in *A. incisivum*.

A left tibia and fibula (Pl. 13, fig. 2) but only the right fibula, are labelled as belonging to the skeleton no. 2, R. 1, 1947 ; *Dicerorhinus leakeyi*. The tibia is somewhat laterally flattened in its proximal part, but the distal end is well-preserved. Fortunately the right tibia of the shellaced limb of *Aceratherium acutirostratum*, though laterally flattened, permits a few measurements to be taken, which show it to be slightly shorter than that of *D. leakeyi* (Table 40). A right tibia marked KB.S,

Maboko (= Kiboko) Island, lacks the lateral proximal portion. The proximal portion of a right tibia (M. 18920), marked Rs. 105, Rusinga, the lower two-thirds of a right tibia marked R. 1, Rusinga, the distal end of a right tibia (M. 18919) marked Rs. 31, Rusinga, and that of a left tibia (M. 18918) marked Rs., Rusinga, are the remaining specimens in the collection; measurements so far as possible are recorded in Table 40.

TABLE 40  
Measurements of tibia of *Dicerorhinus* and *Aceratherium* (mm.)

|                               | <i>D. leakeyi</i><br>sin. | <i>A. acuti-</i><br><i>rostratum</i> | KB.S | M. 18920 | R. 1  | M. 18919 | M. 18918 |
|-------------------------------|---------------------------|--------------------------------------|------|----------|-------|----------|----------|
| Greatest length               | 420                       | c. 410                               | 380  | —        | —     | —        | —        |
| Medial length                 | 375                       | c. 370                               | 350  | —        | —     | —        | —        |
| Proximal width                | —                         | —                                    | —    | 125+     | —     | —        | —        |
| Distal width                  | 100                       | —                                    | 82   | —        | 95    | 92       | 95       |
| Distal ant. post.<br>diameter | c. 80                     | —                                    | 79   | —        | c. 80 | 73       | 72       |

  

|                               | <i>D. schleier-</i><br><i>macheri</i> | <i>D. orientalis</i> | <i>D. primaevus</i> | <i>D. sumatrensis</i> | Steinheim |       |
|-------------------------------|---------------------------------------|----------------------|---------------------|-----------------------|-----------|-------|
|                               |                                       |                      |                     |                       | no. 1     | no. 2 |
| Greatest length               | 388                                   | —                    | —                   | 313                   | 340       | 300   |
| Medial length                 | —                                     | 350                  | 340-372             | 282                   | —         | —     |
| Proximal width                | 130                                   | 126                  | 119-130             | 116                   | 110       | 120   |
| Distal width                  | —                                     | 96                   | 98-109              | 82                    | 75        | 100   |
| Distal ant. post.<br>diameter | 68                                    | —                    | —                   | 59                    | —         | —     |

The tibia of *D. schleiermacheri* has a greatest length less than that in *D. leakeyi* (taken from Kaup 1854; the other measurements after Kaup 1834: 44). That of *D. orientalis* (Gaudry 1862-67: 207, pl. 32, fig. 8) is within the limits of eleven (!) tibiae of *D. primaevus* (Arambourg 1959: 71) or nearly so. Of the Steinheim tibiae recorded by Roger (1900: 18) no. 1 is regarded as representing *Aceratherium*, the shorter one (no. 2) is as short as in *Brachypotherium* but not quite so broad; in *Brachypotherium brachypus* the proximal width is one-half the length.

The fibula belonging to the skeleton of *Dicerorhinus leakeyi* no. 2, R. 1, 1947, is longer than the three fibulae recorded from Steinheim by Roger (1900: 18). Of these, that with a length of 280 mm. (see Table 41) is stated to belong to the supposed *Aceratherium* tibia that is 340 mm. in greatest length (Steinheim no. 1 in Table 40); the others must have belonged to even longer tibiae. The preservation of the right fibula of the skeleton of *D. leakeyi* is perfect; it is an enigma to me why the right tibia of the skeleton has not been preserved.

There is an abundance of astragali in the present East African collection: some twenty specimens in all one of which (no. 538, Gumba, Rusinga, 1949) is that of *Brachypotherium* and is dealt with under the head *B. heinzselini* in the present paper. All the others belong to either *Dicerorhinus* or *Aceratherium*.

TABLE 41  
 Measurements of fibula of *Dicerorhinus* and *Aceratherium* (mm.)

|                            | <i>D. leakeyi</i> | <i>D. sumatrensis</i> | Steinheim |     |     |
|----------------------------|-------------------|-----------------------|-----------|-----|-----|
|                            | dext.             |                       |           |     |     |
| Length                     | 350               | 275                   | 280       | 332 | 320 |
| Greatest proximal diameter | 45                | 42                    | —         | —   | —   |
| Greatest distal diameter   | 47                | 39                    | —         | —   | —   |

The following specimens are from the right side :

1. M. 18875, Rs., Rusinga.
2. No. 132, R. 2-4, Rusinga, 1949.
3. F. 3264, R. 4, Rusinga, 1942.
4. M. 18881, Rs. 38, Rusinga.
5. No. 679, R. 106, Rusinga, 1947.
6. M. 18876, Karungu.
7. M. 18878, Karungu.
8. M. 18882, KB. A, Maboko (= Kiboko) Island.
9. K. 382, 1950, Ngira, Karungu.
10. The deformed specimen of the limb of *Aceratherium acutirostratum*.

Those from the left side are as follows :

11. No. 2, R. 1, 1947, of the skeleton of *Dicerorhinus leakeyi* (Pl. 14, fig. 1).
12. M. 18880, Rs., Rusinga.
13. Arongo Chianda, 25. x. 1939.
14. M. 18877, Rs. 21, Rusinga.
15. M. 18879, Rs. 31, Rusinga.
16. Aloir '39, Owen (Pl. 14, fig. 2).
17. No. 528, Kiune, Rusinga, 1949.
18. M. 18883, Rs., Rusinga.
19. No. 1054, S.E. of Kiahera Hill, Rusinga.

Most of the specimens are to some extent damaged, and often the lateral trochlea ridge is incomplete. This is also the case in the astragalus of the *Dicerorhinus leakeyi* skeleton, but in this case the associated calcaneum is preserved and fits on to it perfectly (Pl. 14, fig. 1) so that the lateral height (over the top of the lateral trochlea ridge and the lateral edge of the distal cuboid facet) can be exactly determined. The medial height of the astragalus, which can be almost invariably taken (over the medial trochlea ridge and the distal navicular facet), is usually slightly less than the lateral height. The difference is apparently of no significance, but it has been cited (Wang 1928 : 204) as constituting a probable means of distinction between *Dicerorhinus* and *Aceratherium*. Wang observed that in *Aceratherium* the astragalus would be higher laterally than medially, whereas in *Dicerorhinus* lateral and medial height would be equal, or the medial height greater than the lateral. Now, as will be seen from Table 42, in four out of the ten astragali of which both the lateral and the medial height are known the lateral slightly exceeds the medial height, including that (no. 11) of *D. leakeyi*, which thereby would present the *Aceratherium* character.



Further, the astragalus from Viehhausen associated with a dentition of *Aceratherium tetradactylum* as recorded by Rinnert (1956 : 33, pl. 3, figs. 1, 3) appears to be equally high on both sides, and thereby *Dicerorhinus*-like. Therefore, it seems to me that reliable distinguishing characters for *Dicerorhinus* on the one hand, and *Aceratherium* on the other, are still to be found.

TABLE 42  
Measurements of astragalus of *Dicerorhinus* and *Aceratherium* (mm.)

|                                     |      |      |      |      |      |      |      |      |      |
|-------------------------------------|------|------|------|------|------|------|------|------|------|
| No. of specimen                     | 1    | 2    | 3    | 4    | 5    | 6    | 7    | 8    | 9    |
| Lateral height                      | 66   | —    | 81   | 67   | 67   | —    | —    | 70   | —    |
| Medial height                       | 67   | 71   | 78   | 66   | 71   | 72   | 72   | 72   | 73   |
| Total width                         | 71   | 88   | 89   | 81   | 73   | 85   | 86   | 83   | 80   |
| Ratio medial height/<br>total width | 0.94 | 0.81 | 0.88 | 0.81 | 0.97 | 0.85 | 0.84 | 0.87 | 0.90 |
| Trochlea width                      | 64   | 69   | 78   | 65   | 65   | 67   | 72   | 66   | 67   |
| Width of distal facets              | 69   | 75   | 76   | 73   | 66   | 78   | 71   | 72   | 73   |
| No. of specimen                     | 11   | 12   | 13   | 14   | 15   | 16   | 17   | 18   | 19   |
| Lateral height                      | 90   | 63   | —    | —    | —    | 88   | 71   | 71   | —    |
| Medial height                       | 88   | 67   | 70   | 69   | 73   | 85   | 72   | 72   | 65   |
| Total width                         | 97   | 84   | —    | 81   | —    | 96   | 85   | 84   | —    |
| Ratio medial height/<br>total width | 0.91 | 0.80 | —    | 0.85 | —    | 0.89 | 0.85 | 0.86 | —    |
| Trochlea width                      | 86   | 67   | 70   | 68   | 70   | 84   | 72   | 69   | —    |
| Width of distal facets              | 82   | 73   | 73   | 69   | —    | 77   | 75   | —    | —    |

In the East African specimens the trochlea width (measured over the lateral and medial surfaces) is either less than the medial height or equal to it (in *Brachypotherium* the trochlea width exceeds the medial height). The total width (measured over the medial distal tuberosity and the lateral edge of the trochlea) does not exceed the medial height to the extent seen in *Brachypotherium* (Table 19); the ratio of medial height to total width varies in fifteen specimens from 0.80 to 0.97, as opposed to 0.73 or less in *Brachypotherium*.

The astragalus of *D. schleiermacheri* (Kaup 1834 : 45, pl. 13, fig. 11) is a rather high specimen, the lateral height being given as 85 mm., the trochlea width as 70 mm., and the greatest width as 81 mm. From Kaup's illustrations it seems that the external height has been taken over the ridge between the cuboid and the navicular facet, and that the trochlea width has not been taken over the lateral and medial surfaces but perhaps at the top of the ridges. In the British Museum (Natural History) there is a cast of a right astragalus from Hessen-Darmstadt, M.2786, catalogued as being of the specimen figured by Kaup (1834, pl. 13, fig. 11) as *D. schleiermacheri*. Its measurements are given in Table 43; they correspond well with those of the East African astragali although the trochlea width exceeds the medial height. The astragalus of *D. ringstroemi* (Ringström 1924 : 16, text-fig. 8) is larger than the largest Rusinga specimen; that of *D. primaevus* (Arambourg 1959:

72) in the few measurements given seems to agree well with our no. 3 (F. 3264, from Rusinga). Under *Aceratherium incisivum* Kaup (1834, pl. 15, fig. 2) figures an astragalus from Oppenheim<sup>1</sup> that is relatively much higher than an astragalus from Budenheim (pl. 15, fig. 10). According to the measurements given by Kaup (p. 60) the trochlea width (stated to have been taken over the external and internal surfaces) much exceeds the medial height in the Budenheim specimen, although it evidently does not have the great total width characteristic of *Brachypotherium*. An astragalus from Steinheim recorded by Roger (1900 : 24) as *Aceratherium* is rather high laterally (perhaps measured over the distal ridge between cuboid and navicular facets), but the ratio of medial height to total width is as in various Karungu and Rusinga specimens. The astragalus associated with teeth of *Aceratherium tetradactylum* (Rinnert 1956 : 34, pl. 3, figs. 1, 3) is intermediate between the two *Aceratherium* specimens figured by Kaup in medial height as well as in trochlea width. The one and only definite *Aceratherium* astragalus in our collection (no. 10) cannot be measured because of its poor state of preservation. That from Losodok cautiously identified by Arambourg (1933 : 10) as *Aceratherium?* sp. corresponds with various of our specimens in height and total width (74, and 86 mm., respectively) and, as Arambourg realized, represents either *Aceratherium* or *Dicerorhinus*.

TABLE 43

Measurements of astragalus of *Dicerorhinus* and *Aceratherium* (mm.)

|                                     | <i>D. schleier-<br/>macheri</i> | <i>D. ring-<br/>stroemi</i> | <i>D. prima-<br/>evus</i> | <i>D. suma-<br/>trens</i> | Oppen-<br>heim | Buden-<br>heim | Vieh-<br>hausen | Stein-<br>heim |
|-------------------------------------|---------------------------------|-----------------------------|---------------------------|---------------------------|----------------|----------------|-----------------|----------------|
| Lateral height                      | —                               | —                           | —                         | 66                        | 63             | 71             | —               | 76             |
| Medial height                       | 75                              | —                           | 79                        | 68                        | 61             | 67             | 64              | 66             |
| Total width                         | 93                              | 100                         | 90                        | 82                        | —              | —              | —               | 78             |
| Ratio medial height/<br>total width | 0.81                            | —                           | 0.88                      | 0.83                      | —              | —              | —               | 0.85           |
| Trochlea width                      | 80                              | 89                          | —                         | 70                        | 63             | 77             | 67              | —              |
| Width of distal facets<br>tuber     | 76                              | —                           | —                         | 66                        | 68             | 66             | —               | —              |

In sharp contrast to the abundance of astragali, there are only three specimens of the calcaneum in the East African Miocene collection, the left calcaneum of the skeleton of *Dicerorhinus leakeyi* no. 2, R. 1, 1947, well preserved (Pl. 14, fig. 1), a

<sup>1</sup> The Oppenheim astragalus has the medial and the distal calcaneum facets confluent, which is regarded as typical for *Aceratherium* by Ringström (1924 : 74, text-fig. 43). In the Budenheim astragalus these two facets are separate. The difference is apparently trivial ; there may, or may not, be a shallow non-articular groove between these two facets. In most of the East African astragali the junction area of the medial and distal calcaneum facets is damaged, but in M. 18881 and M. 18882 the two facets are confluent, in no. 679 separate, whereas in the astragalus of *D. leakeyi* there appears to be a very narrow groove between the two, an intermediate condition we see also in *D. sumatrensis*. In two astragali from Steinheim figured by Fraas (1870 : 302, pl. 7, figs. 7, 8) as *Rh. sansaniensis* and *Rh. brachypus* (that is, *Dicerorhinus* and *Brachypotherium*) respectively, the medial and distal calcaneum facets are separate. The larger specimen (pl. 7, fig. 8) agrees in shape and size with *Aceratherium tetradactylum*, while the smaller (pl. 7, fig. 7) may belong to *Dicerorhinus* (Rinnert 1956 : 36). Needless to say, I do not think that the presence or absence of a bridge between the medial and the distal calcaneum facet of an astragalus is more than an individual variation, useless for intergeneric comparison.

much deformed shellaced specimen belonging to the right limb of *Aceratherium acutirostratum*, and no. 679, R. 106, Rusinga, 1947. The last is from the left side but evidently is of the same individual as the right astragalus bearing the same number (no. 5 in Table 42). The tuber and the cuboid facet are not complete, and approximate measurements only can be given.

TABLE 44

Measurements of calcaneum of *Dicerorhinus* and *Aceratherium* (mm.)

|                         | <i>D. leakeyi</i> |         | <i>D. schleier-</i> | <i>D. prima-</i> | <i>D. suma-</i> | Buden- | Vieh-  | Stein- |
|-------------------------|-------------------|---------|---------------------|------------------|-----------------|--------|--------|--------|
|                         | sin.              | no. 679 | <i>macheri</i>      | <i>evus</i>      | <i>trensis</i>  | heim   | hausen | heim   |
| Lateral height          | 148               | —       | 135                 | 132              | 106             | 122    | 110    | 129    |
| Greatest width          | 89                | c. 60   | —                   | 76               | 71              | —      | 71     | 82     |
| Ant. post. cuboid facet | 48                | c. 40   | 48                  | —                | 39              | 48     | —      | —      |
| Transv. cuboid facet    | c. 25             | —       | 24                  | —                | 23              | 21     | —      | —      |
| Greatest diameter tuber | 73                | c. 60   | 71                  | —                | 63              | 81     | 57     | —      |
| Transv. diameter tuber  | 54                | —       | 52                  | —                | 46              | 45     | —      | 46     |

The calcaneum of *D. schleiermacheri* (Kaup 1834 : 45, pl. 13, fig. 10) appears to correspond well with that of *D. leakeyi*; the Rusinga bone is only somewhat longer. The greatest width of the Eppelsheim specimen is about 80 mm. That of *D. primaevus*, the length and width only of which are known, is smaller though it is near to the calcaneum from Steinheim recorded by Roger (1900 : 23) (which is perhaps the same as the specimen figured by Fraas 1870, pl. 7, fig. 10). The bone in question, figured as *Rh. sansaniensis* (hence, *Dicerorhinus*), is considered indistinguishable from that of *Aceratherium tetradactylum* by Rinnert (1956 : 36). The Budenheim calcaneum ascribed to *Aceratherium incisivum* (Kaup 1834 : 60, pl. 15, fig. 11) differs from that of *A. tetradactylum* from Viehhausen figured by Rinnert (1956, pl. 3, figs. 1, 2) only in size and the configuration of the tuber.

Of the skeleton of *Dicerorhinus leakeyi* no. 2, R. 1, 1947, we have the entire left navicular, and also an anterior fragment of the right (separately catalogued under no. 360). There are also two right and two left naviculars, viz.,

M. 18887, R. 1, Rusinga,

M. 25187, Kathwanga, Rusinga, 1947,

No. 64, 1950, R. 1, Rusinga, and

M. 25188, Kathwanga, Rusinga, 1947.

These bones are very similar in shape and differ mainly in dimensions; the navicular of *D. sumatrensis* is only relatively wider (the width of these bones has not been recorded for *D. ringstroemi* (Ringström 1924 : 16, text-fig. 8) or for *D. primaevus*). The navicular of *D. schleiermacheri* (Kaup 1834 : 45) is larger than that in *Aceratherium incisivum* (Kaup 1834 : 60, pl. 15, fig. 9a-c), which is similar in size to that of the recent species; its total width is about 50 mm.

TABLE 45

Measurements of navicular of *Dicerorhinus* and *Aceratherium* (mm.)

|                          | <i>D. leakeyi</i> | M. 18887              | M. 25187              | no. 64 | M. 25188            | <i>D. primaevus</i> |
|--------------------------|-------------------|-----------------------|-----------------------|--------|---------------------|---------------------|
| Greatest anterior height | 31                | 31                    | 26                    | 25     | 20                  | 30                  |
| Total width              | 49                | 52                    | 47                    | 47     | 44                  | —                   |
| Ant. post. diameter      | 69                | 71                    | 60                    | 64     | 54                  | 60                  |
|                          |                   |                       |                       |        | <i>Aceratherium</i> |                     |
|                          |                   | <i>D. ringstroemi</i> | <i>D. sumatrensis</i> |        | <i>incisivum</i>    |                     |
| Greatest anterior height |                   | 27                    | 20                    |        | —                   |                     |
| Total width              |                   | —                     | 50                    |        | —                   |                     |
| Ant. post. diameter      |                   | 75                    | 54                    |        | 56                  |                     |

There is the left cuboid of the skeleton of *Dicerorhinus leakeyi* no. 2, R. 1, 1947 (Pl. 13, figs. 4, 5) and in addition no less than eight isolated cuboids, six right and two left :

- M. 18892, Karungu,
- M. 18890, R. 1, Rusinga (Pl. 13, fig. 6).
- M. 18891, Kachuku, Lower Series, Karungu,
- No. 440, Ngira, Karungu,
- M. 18894, Rs. 105, Rusinga,
- M. 18893, R. 8, Rusinga,
- M. 18895, Kachuku, Karungu, and
- M. 18889, Rs., Rusinga.

These cuboids appear to fall into two groups, viz., one in which the anterior height is nearly equal to the anterior width, and one (M. 18890 and M. 18893) in which the anterior surface is distinctly higher than wide (Table 46). In *Brachypotherium* the

TABLE 46

Measurements of cuboid of *Dicerorhinus* and *Aceratherium* (mm.)

|                              | <i>D. leakeyi</i> | M. 18892 | M. 18890            | M. 18891              | no. 440 | M. 18894            | M. 18893 |
|------------------------------|-------------------|----------|---------------------|-----------------------|---------|---------------------|----------|
| Anterior height              | 48                | 48       | 46                  | 42                    | 41      | 41                  | 36       |
| Anterior width               | 47                | 47       | 36                  | 43                    | 42      | 40                  | 30       |
| Greatest ant. post. diameter | 64                | 73       | 63                  | 69                    | —       | c. 65               | 66       |
|                              |                   |          |                     |                       |         | <i>Aceratherium</i> |          |
|                              | M. 18895          | M. 18889 | <i>D. primaevus</i> | <i>D. sumatrensis</i> | (Roger) | (Rinnert)           |          |
| Anterior height              | 40                | 34       | 48                  | 40                    | 46      | 40                  |          |
| Anterior width               | 37                | 35       | 39                  | 40                    | 34      | 30                  |          |
| Greatest ant. post. diameter | —                 | —        | —                   | 56                    | —       | —                   |          |

cuboid is distinctly wider than high anteriorly (Roger 1900 : 24) ; the present specimens represent either *Dicerorhinus* or *Aceratherium*. In *D. schleiermacheri* the anterior height of the cuboid is equal to the anterior width (Kaup 1834 : 45), and so it

is in the cuboid of *D. leakeyi* and in that of Recent *D. sumatrensis*. However, the cuboid of *D. primaevus* as appears both from the measurements and from the illustration (Arambourg 1959 : 72, text-fig. 32B) is decidedly higher than wide. This is also the case in the Steinheim *Aceratherium* recorded by Roger (1900 : 24) and in *Aceratherium tetradactylum* from Viehhausen (Rinnert 1956 : 34, pl. 3, fig. 1). In *A. incisivum* (Kaup 1834 : 45, pl. 15, fig. 9) the anterior width of the cuboid appears to be somewhat greater than the height. Therefore, it would seem that the relative height of the cuboid cannot be used in intergeneric differentiation.

Both ectocuneiforms of the skeleton of *Dicerorhinus leakeyi* no. 2, R. 1, 1947, are available. There are four other ectocuneiforms, all from the right side :

- M. 18905, R. 1, Rusinga,
- M. 18886, Rs. 105, Rusinga,
- M. 18885, Rs. 30, Rusinga, and
- M. 18888, Rs., Rusinga.

Of these, M. 18905 fits on to the navicular M. 18887, and belongs to the same individual. It is higher, but not wider than the ectocuneiform of *D. leakeyi* (Table 47). The ectocuneiform of *D. sumatrensis* is less elongated anteroposteriorly than the fossil bones. That of *D. primaevus* (Arambourg 1959 : 72) appears to be rather low ; the width, given as 23 mm., is omitted in the Table as it is probably a misprint (53?).

TABLE 47

Measurements of ectocuneiform of *Dicerorhinus* and *Aceratherium* (mm.)

|                     | <i>D. leakeyi</i> | M. 18905 | M. 18886 | M. 18885 | M. 18888 | <i>D. primaevus</i> | <i>D. sumatrensis</i> |
|---------------------|-------------------|----------|----------|----------|----------|---------------------|-----------------------|
| Anterior height     | 27                | 31       | 26       | 26       | 25       | 21.5                | 24                    |
| Anterior width      | 55                | 51       | 50       | 44       | 43       | —                   | 47                    |
| Ant. post. diameter | 53                | 51       | 52       | 50       | 48       | 60                  | 43                    |

Only the right mesocuneiform of the skeleton of *Dicerorhinus leakeyi* no. 2, R. 1, 1947, has been saved. It is more elongated anteroposteriorly than that in *D. sumatrensis* (Table 48).

TABLE 48

Measurements of mesocuneiform of *Dicerorhinus* (mm.)

|                     | <i>D. leakeyi</i> | <i>D. primaevus</i> | <i>D. sumatrensis</i> |
|---------------------|-------------------|---------------------|-----------------------|
| Height              | 19                | 21                  | 16                    |
| Width               | 22                | 26                  | 19                    |
| Ant. post. diameter | 41                | —                   | 29                    |

The left entocuneiform only of the skeleton of *Dicerorhinus leakeyi* no. 2, R. 1, 1947, is available ; the proximal portion articulating with navicular and mesocuneiform has broken off, and only the facet for Mt. II remains. The posterior

tuberosity is much larger than that in the entocuneiform of *D. sumatrensis* (in parentheses) : height 47 mm. (27 mm.), and width 30 mm. (22 mm.).

All the metatarsals from the left side, as well as the Mt. II and IV from the right side of the skeleton of *Dicerorhinus leakeyi* no. 2, R. 1, 1947, are preserved (Pl. 13, fig. 3; Pl. 15). No other entire metatarsals are in the East African Miocene collection. Roger (1900 : 41) has tried to separate the metatarsal IV of *Dicerorhinus* from that of *Aceratherium*, and states that Mt. IV in *Aceratherium* has a postero-lateral incurvation of the large proximal cuboid facet, which makes this facet trilobate or trefoil-shaped, with the shaft forming a prominence behind the incurvation, whereas in Mt. IV of *Dicerorhinus* the cuboid facet is distinctly narrower and more antero-posteriorly elongated. My observations do not bear this out; on the contrary the cuboid facet on Mt. IV in *Dicerorhinus sumatrensis* and that in *D. leakeyi* answer to the description of the facet of Roger's *Aceratherium*, and the cuboid facet of Mt. IV of *Aceratherium tetradactylum* associated with the dentition at Viehhausen is described by Rinnert (1956 : 34) as broadly elliptical.

The right second metatarsal of the *D. leakeyi* skeleton shows an interesting pathological condition (Pl. 15, figs. 1-3). The distal half is thickened, and the distal articulation wholly deformed. The swollen surface shows irregular growths all over and appears spongy. Without radiological or histological examination the attribution of such an affection of the bone to a specific disease is impossible, but the outward appearance of the fossil is suggestive of something like Paget's disease. No other bones of the skeleton (nor the skull so far as preserved) appear to be afflicted with this disease (which may occur quite localized in the human skeleton); it may have developed of course in some of the missing elements like the metacarpals or the right tibia. The phalanges of this digit were certainly affected, but these are not present in the collection.

The metatarsals of *D. leakeyi* are remarkable for their length. Mt. IV is longer than the Mc. IV of *Dicerorhinus* or *Aceratherium* from the same Rusinga deposits (M. 18814). In *D. primaevus* (Arambourg 1959 : 72 and 68) Mt. IV is longer than Mc. IV although Mt. III is shorter than Mc. III. In *D. sumatrensis* there is only a slight difference in length between Mt. IV and Mc. IV. In general, metatarsals are more shortened than the metacarpals within the same species.

The metatarsals of *D. schleiermacheri* are unknown; its metacarpals, however, are longer than those in *orientalis*, *ringstroemi*, and *primaevus*, and probably would have exceeded those of *D. leakeyi* in length. An Mt. III of *D. orientalis* from Pikermi recorded by Gaudry (1862-67 : 207, pl. 32, fig. 9) has a length only of 160 mm. by a greatest distal width of 52 mm., less than in *D. leakeyi*. The metatarsals of *D. primaevus* are also shorter than those of *D. leakeyi*. Mt. II and Mt. IV of *D. primaevus* are relatively less expanded distally than in *D. sumatrensis*, as is also the case with Mt. II and Mt. IV of *D. leakeyi*. In all three forms the median metatarsal is approximately 10% longer than the metatarsals on either side of it, as it is in *Aceratherium incisivum* recorded by Ringström (1924 : 192) and listed in the last column of Table 49. In a set of metatarsals from Budenheim recorded as *A. incisivum* by Kaup (1834 : 61, pl. 15, fig. 9) the lengths are less than those studied by Ringström.

TABLE 49

Measurements of metatarsals of *Dicerorhinus* and *Aceratherium* (mm.)

|                            | <i>D. leakeyi</i> | <i>D. primaevus</i> | <i>D. sumatrensis</i> | <i>Aceratherium</i> ? sp.<br>Losodok | Viehhausen | Freimann | Budenheim | (Ringström) |
|----------------------------|-------------------|---------------------|-----------------------|--------------------------------------|------------|----------|-----------|-------------|
| Mt. II, median length      | 162               | 149                 | 126                   | —                                    | 140        | —        | 135       | 146         |
| Proximal width             | 29                | —                   | 29                    | —                                    | 21         | —        | —         | —           |
| Prox. ant. post. diameter  | 48                | —                   | 34                    | —                                    | 36         | —        | —         | —           |
| Middle width               | 32                | —                   | 30                    | —                                    | 23         | —        | —         | 30          |
| Middle ant. post. diameter | 30                | —                   | 21                    | —                                    | 20         | —        | —         | —           |
| Greatest distal width      | 42                | 35                  | 40                    | —                                    | —          | —        | —         | —           |
| Width of distal trochlea   | 36                | —                   | 35                    | —                                    | 26.5       | —        | —         | —           |
| Distal ant. post. diameter | 41                | —                   | 39                    | —                                    | 33         | —        | —         | —           |
| Ratio middle width/length  | 0.20              | —                   | 0.24                  | —                                    | 0.16       | —        | —         | 0.21        |
| Mt. III, median length     | 180               | 165                 | 144                   | 168                                  | —          | —        | 150       | 158         |
| Proximal width             | 57                | —                   | 53                    | —                                    | —          | —        | —         | —           |
| Prox. ant. post. diameter  | 49                | —                   | 37                    | —                                    | —          | —        | —         | —           |
| Middle width               | 50                | —                   | 41                    | 42                                   | —          | —        | —         | 35          |
| Middle ant. post. diameter | 25                | —                   | 19                    | —                                    | —          | —        | —         | —           |
| Greatest distal width      | c. 60             | 52                  | 53                    | 46                                   | —          | —        | —         | —           |
| Width of distal trochlea   | 51                | —                   | 44                    | —                                    | —          | —        | —         | —           |
| Distal ant. post. diameter | 41                | —                   | 38                    | —                                    | —          | —        | —         | —           |
| Ratio middle width/length  | 0.28              | —                   | 0.28                  | 0.25                                 | —          | —        | —         | 0.22        |
| Mt. IV, median length      | 160               | 147                 | 126                   | 160                                  | 140        | 126      | 140       | 145         |
| Proximal width             | 44                | —                   | 41                    | —                                    | 33         | 40       | —         | —           |
| Prox. ant. post. diameter  | 46                | —                   | 41                    | —                                    | 36         | 36+      | —         | —           |
| Middle width               | 29                | —                   | 25                    | 33                                   | 21         | 28       | —         | —           |
| Middle ant. post. diameter | —                 | —                   | 21                    | —                                    | 25         | 23       | —         | —           |
| Greatest distal width      | 38                | 38                  | 37                    | 39                                   | —          | —        | —         | —           |
| Width of distal trochlea   | 37                | —                   | 32                    | —                                    | 25         | 30       | —         | —           |
| Distal ant. post. diameter | 40                | —                   | 38                    | —                                    | 32         | 33       | —         | —           |
| Ratio middle width/length  | 0.18              | —                   | 0.20                  | 0.21                                 | 0.15       | 0.22     | —         | —           |

The Mt. III and Mt. IV from Losodok described by Arambourg (1933: 11, pl. 1, figs. 4, 5) were noted to be nearly identical in dimensions with those of *Aceratherium tetradactylum*, but differing in their wider extremities and the shape of their articular surfaces. The fourth metatarsal Arambourg noted to be longer and more slender than that in the Sansan *Aceratherium (tetradactylum)*. Arambourg (1933) preferred to leave the generic identity of the Losodok bones uncertain, naming them "*Aceratherium?* sp.". The Mt. IV of *D. leakeyi*, it will be observed, corresponds with its homologue from Losodok in length and distal width, but has a more slender shaft.

The Rusinga Mt. IV is intermediate in relative shaft width between a slender Mt. IV of *Aceratherium tetradactylum* from Viehhausen (Rinnert 1956: 34) and one from Freimann recorded by Stromer (1928: 29) as probably referable to *A. tetradactylum*. In the Aquitanian of Laugnac there is a very slender Mt. IV figured by Repelin (1917: 40, pl. 6, figs. 3, 4) as "un type spécial de Rhinocérotidé" that has a great resemblance to the same bone in *A. tetradactylum* (which is Vindobonian); its length is 130 mm., and its middle width only 20 mm., giving a ratio of 0.15. The Laugnac bone is found in the same deposits as *Aceratherium lemanense* (= *Teleoceras aginense* Repelin: Lavocat 1951: 114) that has less slender metapodials (Mt. IV length 99-103 mm., middle width 28-30 mm.). The Mt. III from Losodok nearly falls within the range of length of this bone in *A. tetradactylum* as given by Osborn (1900: 246: Mt. III 135-165 mm.); the Rusinga Mt. III is longer but relatively less slender. The Rusinga Mt. II is again less slender than that from Viehhausen recorded by Rinnert (1956: 34, pl. 3, fig. 4), but is about equal in relative shaft width to that of *A. incisivum* as given by Ringström. A right Mt. II from the Upper Burdigalian of La Romieu figured by Roman & Viret (1934: 36, pl. 9, fig. 12) is about 128 mm. in median length and very slender (no measurement given), just as is that from Viehhausen. The La Romieu bone has been identified only as "*Ceratorhinus* sp.?"

The conclusions from all this may only be that we are not able as yet to distinguish between the metapodials of *Dicerorhinus* and *Aceratherium*.

Two proximal portions of right second metacarpals have to be recorded, viz., M. 18844, R. 1, Rusinga (proximal width 32 mm., ant. post. 46 mm.), and M. 18847, Rs. 105, Rusinga (proximal width 29 mm., ant. post. 49 mm.). These bones are very much like their homologue in the skeleton of *D. leakeyi*.

All of the phalanges of the left hind foot of the skeleton of *Dicerorhinus leakeyi* no. 2, R. 1, 1947, are present (Pl. 13, fig. 3), and only the third phalanx of the median digit is incomplete. Of the right hind foot there are the first and second phalanges of the median digit (Pl. 10, figs. 4, 5), and none of the other digits. Measurements will be found in Table 50.

TABLE 50  
Measurements of posterior phalanges of *Dicerorhinus* (mm.)

|                     | <i>D. leakeyi</i> |     |    | <i>D. primaevus</i><br>lateral<br>digit | <i>D. sumatrensis</i> |     |    |
|---------------------|-------------------|-----|----|---|-----------------------|-----|----|
|                     | I                 | III | IV |   | II                    | III | IV |
| Phalanx I, length   | 37                | 40  | 33 | 42                                      | 31                    | 35  | 30 |
| Proximal width      | 40                | 55  | 38 | 48                                      | 38                    | 47  | 35 |
| Phalanx II, length  | 27                | 31  | 25 | 37                                      | 23                    | 27  | 22 |
| Proximal width      | 37                | 58  | 35 | 33                                      | 33                    | 48  | 32 |
| Phalanx III, length | 33                | —   | 30 |   |                       |     |    |
| Greatest diameter   | 60                | —   | 58 |   |                       |     |    |

In *D. leakeyi* as well as in *D. sumatrensis* the phalanges of digit IV are smaller than those of digit II. The width of the second phalanx of the lateral digit of *D. primaevus*



(Arambourg 1959 : 69) is probably 43 instead of 33 mm. Comparison with Table 37, in which the measurements of the anterior phalanges are given, shows that the lateral digit phalanges are more reduced in size relative to those of the median digit in the hind foot than in the fore foot.

To end the account of the foot skeleton of *Dicerorhinus leakeyi* mention should be made of the sesamoids. Some of the proximal sesamoid bones of the left hind foot are preserved *in situ*. The two situated behind the distal end of metatarsal III are 41 mm. long and 22 mm. wide ; those attached to metatarsal II are 32 mm. long by a width of 17 mm. In *D. sumatrensis* the proximal sesamoids have the same width (17 mm.) ; those of the median digit are 38 mm. long, and those of the second digit 30 mm.

There remains a number of distal ends of metapodials, phalanges, and sesamoid bones enumerated here for the sake of completeness. The specimens definitely belonging to *Brachypotherium* have been sorted, and are recorded under *B. heinzellini*. Those listed in the following pages are either *Dicerorhinus* or *Aceratherium*.

#### Distal ends of median metapodials (measurements in mm.)

|                                 | Greatest width | Trochlea width | Ant. post. diameter |
|---------------------------------|----------------|----------------|---------------------|
| No. 430, Karungu, 1947          | 57             | 45             | —                   |
| M. 18818, Rusinga               | —              | 45             | 38                  |
| M. 18823, Rs. 101, Rusinga      | —              | 51             | —                   |
| M. 18836, Ombo                  | c. 53          | c. 44          | 41                  |
| M. 18834, marked N <sub>1</sub> | 58             | 48             | 42                  |

#### Distal ends of lateral metapodials

|   |    |       |    |
|---|----|-------|----|
| M. 18829, R. 1, Rusinga                     | 38 | 34    | —  |
| M. 18825, Rusinga                           | 38 | 35    | 32 |
| M. 18826, Rs. 31, Rusinga                   | 39 | 37    | 34 |
| M. 18821, Rusinga                           | —  | 34    | 31 |
| M. 18824, Rusinga                           | 39 | 34    | 34 |
| M. 18820, Rusinga                           | —  | —     | 39 |
| M. 18832, R. 1, Rusinga                     | —  | 41    | 39 |
| M. 18819, Rs. 81, Rusinga                   | —  | 35    | —  |
| M. 18833, R. 1, Rusinga                     | 43 | 40    | 39 |
| M. 18816, Rs. 31, Rusinga                   | 38 | 35    | 36 |
| M. 18817, Rs. 31, Rusinga                   | —  | c. 39 | —  |
| M. 18831, Rusinga                           | —  | 32    | 33 |
| M. 18827, Rs. 105, Rusinga                  | 42 | 38    | 40 |
| M. 18815, R. 2, Rusinga                     | —  | 39    | 43 |
| M. 18828, Rs. 3, Rusinga                    | 40 | 35    | 35 |
| M. 18835, Kachuku, Lower Series,<br>Karungu | —  | 33    | —  |
| M. 18830, Rusinga                           | —  | 34    | 32 |

## Phalanx I, median digit (measurements in mm.)

|  | Length | Prox. width |
|--|--------|-------------|
| M. 18858, R. 1, Rusinga                    | 38     | 55          |
| No. 938, 1947, Gumba red-beds, Rusinga     | 34     | 55          |
| No. 197, 1947, S. of Kiahera Hill, Rusinga | 33     | 52          |
| No. 237, 1950, R. 2-4, Rusinga             | 37     | 48          |
| M. 18860, Rs. 31, Rusinga                  | 34     | 48          |

## Phalanx II, median digit

|   |    |    |
|---|----|----|
| M. 18863, Rs. 30, Rusinga               | 27 | 48 |
| M. 18861, Rusinga                       | 29 | 43 |
| M. 18864, Rs. 30, Rusinga               | 24 | 53 |
| M. 18867, Ngira, Karungu                | 25 | 42 |
| No. 1060, S.E. of Kiahera Hill, Rusinga | 22 | —  |

## Phalanx I, lateral digit

|                                 | Length | Prox. width |
|---------------------------------|--------|-------------|
| M. 18856, Rusinga               | 36     | 38          |
| M. 18857, Rusinga               | 35     | 38          |
| No. 1152, R. 2-4, Rusinga, 1950 | 29     | 35          |
| M. 18853, Rs. 31, Rusinga       | 28     | 40          |
| M. 18868, Ngira, Karungu        | 31     | 39          |

## Phalanx II, lateral digit

|                                   |    |    |
|-----------------------------------|----|----|
| M. 18855, Rs. 104, Rusinga        | 24 | 36 |
| M. 18866, Rs. 30, Rusinga         | 22 | 37 |
| M. 18865, Rusinga                 | 21 | 27 |
| No. 110, 1949, W. Hiwegi, Rusinga | 22 | 29 |

There remain one third phalanx of a median digit, no. 498, Rusinga, 1950 (length 24 mm., greatest width 63 mm.), a third phalanx of a lateral digit, M. 18852, Rusinga (length 40 mm., greatest diameter 64 mm.), and an incomplete third phalanx of a lateral digit, no. 845, Kathwanga, Rusinga (length 29 mm.).

## Proximal sesamoids, median digit

|   | Length | Width |
|---|--------|-------|
| M. 18871, Rusinga   | 48     | 25    |
| No. 921, 1947, N. of Kiahera Hill, Rusinga                  | 49     | 26    |
| M. 18869, Rs. 6a, Rusinga                                   | 47     | 25    |
| M. 18874, Rs. 21, Rusinga                                   | 45     | 24    |
| No. 238, 1950, R. 2-4, Rusinga                              | 43     | 26    |
| M. 18870, R. 1, Rusinga                                     | 40     | 21    |
| No. 536, Chianda Uyoma                                      | 40     | 24    |
| M. 18873, Rs. 21, Rusinga                                   | —      | 23    |
| No. ? (possibly belonging to skeleton no. 2, R. 1,<br>1947) | 40     | 21    |

## Proximal sesamoids, lateral digit

|   |    |    |
|---|----|----|
| No. 239, 1950, R. 2-4, Rusinga                                      | 34 | 16 |
| M. 18872, Rs. 38, Rusinga   | 32 | 17 |
| No. 820, 1947 (possibly belonging to skeleton no. 2,<br>R. 1, 1947) | 31 | 20 |
| No. 820, 1947 (idem, second specimen)                               | 30 | 18 |
| No. ? (idem)  | 30 | 17 |
| No. ? (idem)  | 31 | 16 |

What is probably the distal sesamoid (situated behind the junction of the second and third phalanges) of the median digit (unnumbered, possibly belonging to skeleton no. 2, R. 1, 1947) is 31 mm. wide transversely and 7 mm. high at the articular surface.

The tail vertebrae labelled as belonging to the skeleton no. 2, R. 1, 1947, of *Diceros rhinus leakeyi* range from what is probably the fourth from the sacrum to nearly the last. The largest vertebra has only the left transverse process, 42 mm. in antero-posterior diameter (23 mm. in *D. sumatrensis*), and an arch that appears to have been higher than the body but crushed dorso-ventrally. The spinous process has a thickened summit. The greatest width of the vertebra is about 95 mm. (73 mm.). The second largest caudal vertebra has both transverse processes, greatest width 82 mm. (69 mm.), but these processes are much reduced anteroposteriorly to 21 mm. (14 mm.). The small and distorted arch is bifid behind, and probably not higher than the body.

An isolated double summit of an arch intermediate in size between the last and the vertebrae to be mentioned next indicates that the body of at least one caudal vertebra has been lost. The next has a body still as long as that of the second largest of the lot, viz., 39 mm. (29 mm.), only traces of a transverse process, and a very small arch, which was probably open dorsally. This vertebra is crushed laterally.

Of the remaining thirteen caudal vertebrae only the largest two have two ridges dorsally, the others being without a trace of an arch. These vertebrae are not distorted and seem to form an unbroken series. The length and anterior height of the body decrease from 35 and 27 mm. in the first, over 26 and 12 mm. in the middle (seventh) of the series, to 16 and 8 mm. in the last. The caudal vertebra in *D. sumatrensis* that shows the same reduction of the arch as the anterior of our series of thirteen is the ninth caudal; it is 25 mm. long and 23 mm. high anteriorly. The fifteenth caudal vertebra in *D. sumatrensis* is 26 mm. long and 14 mm. high, while the twenty-first is 19 mm. long and 7 mm. high. It is followed by three more vertebrae, the last one of which has a pointed end.

From this comparison it follows that the tail vertebrae of *D. leakeyi* reduce in length more rapidly as one passes along the series than in the corresponding section of the tail of *D. sumatrensis*, that the relative anterior height is greater half-way along the tail in *D. sumatrensis*, but that it diminishes more rapidly toward the end than in *D. leakeyi*.

## III. DISTRIBUTION OF RHINOCEROSSES OVER EAST AFRICAN MIOCENE SITES

In Table 5I are given the locality records of those specimens of which the generic position has been determined.

TABLE 5I

Distribution of Rhinocerotidae in the East African Miocene

|                                    | <i>Dicerorhinus</i> | <i>Aceratherium</i> | <i>Brachypotherium</i> | <i>Chilotherium</i> |
|------------------------------------|---------------------|---------------------|------------------------|---------------------|
| Rusinga<br>(no sub-site given)     | ×                   | ×                   | ×                      | .                   |
| R. 1                               | ×                   | ×                   | ×                      | .                   |
| R. 1-1a                            | ×                   | .                   | ×                      | .                   |
| R. 2                               | ×                   | .                   | .                      | .                   |
| R. 2-4                             | ×                   | ×                   | .                      | .                   |
| Rs. 3                              | ×                   | .                   | .                      | .                   |
| Rs. 6a                             | .                   | .                   | ×                      | .                   |
| R. 7, Rs. 7                        | .                   | .                   | ×                      | .                   |
| R. 11                              | ×                   | .                   | .                      | .                   |
| Rs. 26                             | ×                   | .                   | .                      | .                   |
| R. 73                              | .                   | .                   | ×                      | .                   |
| Rs. 91                             | .                   | ×                   | .                      | .                   |
| Rs. 101                            | .                   | .                   | ×                      | .                   |
| R. 107                             | .                   | ×                   | .                      | .                   |
| Rs. 108                            | ×                   | .                   | .                      | .                   |
| Gumba                              | ×                   | ×                   | ×                      | ×                   |
| West side of Hiwegi                | ×                   | .                   | ×                      | .                   |
| Kamasengere                        | .                   | ×                   | .                      | .                   |
| Kathwanga                          | ×                   | .                   | ×                      | .                   |
| S. of Kiahera Hill                 | .                   | ×                   | .                      | .                   |
| S.E. of Kiahera Hill               | .                   | .                   | ×                      | .                   |
| Wakundu                            | .                   | .                   | .                      | ×                   |
| Karungu (Andrews<br>1914 and 1937) | .                   | .                   | ×                      | .                   |
| Ngira, Karungu                     | .                   | ×                   | ×                      | .                   |
| Songhor                            | ×                   | .                   | .                      | .                   |
| Moruaret Hill<br>(Deraniyagala)    | .                   | ×                   | .                      | .                   |
| Loperot                            | .                   | .                   | .                      | ×                   |
| Napak I                            | .                   | ×                   | .                      | .                   |
| II A and C                         | .                   | .                   | ×                      | .                   |
| V                                  | ×                   | .                   | .                      | .                   |
| VI                                 | ×                   | .                   | .                      | .                   |

Generically uncertain material of Rhinocerotidae has also been obtained from sub-sites of Rusinga and other sites in Kenya whence no generically identifiable rhinoceros specimens have come, as follows :

R. 4 (astragalus), R. 8 (cuboid), Rs. 21 (radius, astragalus, two proximal sesamoids), Rs. 23a (scapula), Rs. 30 (ectocuneiform, two phalanges II of median digits, phalanx II of lateral digit), Rs. 31 (radius, unciform, Mc. III-IV, patella, tibia, astragalus, three lateral metapodials, phalanx I of median digit, phalanx II of lateral digit), Rs. 38 (astragalus, proximal sesamoid), Rs. 81 (lateral metapodial), Rs. 103 (Mc. III), Rs. 104 (phalanx II of lateral digit), Rs. 105 (Mc. II, tibia, cuboid, ectocuneiform, lateral metapodial), R. 106 (astragalus, calcaneum), Kiahera Hill (P<sub>2</sub>), N. of Kiahera Hill (proximal sesamoid), Kiangata (lower C), Kiune (astragalus),

and the following sites other than Rusinga : Aloir, 1939 (mandibular ramus and astragalus), Chianda Uyoma (proximal sesamoid), Ombo (median metapodial), Maboko (= Kiboko) Island (two scaphoids, tibia, astragalus), Kachuku, Lower Series, Karungu (Mc. II-III, cuboid, lateral metapodial), Kachuku, Karungu (cuboid), Losodok (Arambourg, 1933) (lower M, axis, astragalus, Mt. III-IV, three phalanges I of median and lateral digits), and Arongo Chianda, 25.x.1939 (astragalus).

I have not seen any material from Tambach, and am unable to confirm the record of rhinoceros from that locality (cf. Le Gros Clark & Leakey 1951 : 5). In addition to the nine sites in Kenya from which Rhinocerotidae have been recorded in 1951 there are Aloir, 1939, and Arongo Chianda, 25.x.1939, both with a generically unidentifiable non-brachypothere astragalus. All groups of mammals found in Rusinga are known to be represented at Mfwanganu Island, Kenya, except for the rhinoceroses and insectivores (Whitworth 1961), and indeed the only rhinoceros-like specimen that I have seen from that island, a proximal metapodial fragment, is *Brachyodus aequatorialis* MacInnes, the large Rusinga anthracothere, which will be reported later.

#### IV. TIME PLACEMENT OF THE MIOCENE EAST AFRICAN FAUNAS

The Miocene faunas of East Africa are generally regarded as Early Miocene, corresponding to the Burdigalian stage of Europe. Dr. Leakey kindly informs me that the geology of Rusinga is much more complicated than had been previously thought, and not all of it may be of the same age. Loperot, at present being investigated by the Harvard Expedition, is a considerable area with many different sites that may not be contemporaneous. Most of the Loperot sites are probably much younger than most of Rusinga. Further studies on elements of the *Proconsul* fauna are being undertaken. Potassium-Argon dates have been published during the last few years, and are still being worked on, and these have not invariably had the mammalian palaeontologists' approval.

From a number of K/A dates for Rusinga, including two of over 100 million years (!), Evernden, Savage, Curtis & James (1964 : 176 : KA 336) consider  $15.3 \pm 1.5$  million years the best estimate and only meaningful age ; this would approximately correspond with Late Miocene (Vindobonian). However, the age that has recently been determined for Napak, Uganda, viz.,  $19 \pm 2$  million years (Bishop 1964) points to Early Miocene (Burdigalian). A Middle Miocene age for Rusinga has been proposed on faunal grounds by Thenius (1959 : 268), and the geological setting of the Western Rift deposits of Congo, whence a typical Rusinga fauna has been described (Hooijer 1963), even leaves room for a Late Miocene age of part of the fauna. The slightly different faunules of Malembe and Bololo in the Atlantic coastal region of Congo are Burdigalian as the associated fish fauna indicates (Hooijer 1963 : 5, 64). Radiometric dates are not as yet available for the various Western and Eastern Congo sites.

What now is the bearing of the Rhinocerotidae of Rusinga and Napak on the problem of the age of these deposits? Let us summarize the salient characters and similarities to European Tertiary rhinoceroses.

Of the four genera and species of Rhinocerotidae from Rusinga and other Miocene sites in East Africa two are in keeping with either Burdigalian or Vindobonian, and two rather with Vindobonian, in the European sense. *Aceratherium acutirostratum* is unique in the combination of a shallow naso-maxillary notch (Aquitanian in Europe) and an elevated occiput (Pontian in Europe). Its teeth are more advanced in structure than those in the European Oligocene forms; either Burdigalian or Vindobonian would seem fitting for this species. *Chilotherium*, now found for the first time in Africa (the two Rusinga M need not be specifically the same as the Loperot M<sup>3</sup>)<sup>1</sup>, ranging from Burdigalian into the Pontian in Asia and from Vindobonian into Pontian in Europe, could be either Burdigalian or Vindobonian as well; the earliest chilothers are as fully-fledged as the Pontian (Cooper 1934: 596). *Dicerorhinus leakeyi* has the skull shape of the Vindobonian *D. sansaniensis* although it is larger, and its teeth agree in characters with those of this as well as some larger Pontian forms. It has no close relationship with tapir-sized, slender-footed Aquitanian and Burdigalian *D. tagicus*. *Brachypotherium heinzeli* almost duplicates the Late Vindobonian *B. brachypus*; only its lateral metacarpals are relatively shorter and wider. It is definitely more advanced in progressive metapodial abbreviation than the Moghara *B. snowi*, which has only reached the stage of the Late Burdigalian and Early Vindobonian *B. stehlini*. The four forms occur together in the Gumba beds of Rusinga.

The same assemblage of rhinoceroses, except for the rarest *Chilotherium* sp., occurs at Napak, K/A dated as Early Miocene, Burdigalian. The fauna of Napak is exceedingly similar to that of the Kenya sites; in the latest survey of the fauna (Bishop 1962) this was brought out by various specialists. Rhinocerotidae and Anthracotheriidae were not mentioned in the 1962 paper as no data were available at the time. Among the dental material from Napak kindly sent to me from time to time by Dr. W. W. Bishop there is a very characteristic upper molar of *Brachyodus aequatorialis* MacInnes (1951), indistinguishable from the Rusinga type. The specimen originates from Napak II C, and other from Napak V and VIII, and from Moroto I and II; this will be described later. Thus, the faunal likeness between Napak and Rusinga is further enhanced by the Anthracotheriidae as well as by the Rhinocerotidae.

The fauna of Fort Ternan, a site already famous for *Kenyapithecus wickeri* Leakey (1962), more advanced than *Proconsul*, has a totally different aspect. It comprises a small *Trilophodon* and a suid more evolved than the Rusinga forms, ruminants with incipient horns (unknown in the Miocene), and a highly intriguing form transitional between *Brachyodus* and hippo (Leakey, in Howell & Bourlière (editors), 1963: 554). Anthracotheres are considered ancestral to hippopotami; for these animals no other ancestry can be made plausible. *Brachyodus* occurs in the Burdigalian of Europe, and the first *Hippopotamus* appears in the Pontian of Europe (Hooijer 1946c; Aguirre 1963). The Fort Ternan anthracothere or ancestral hippopotamus, therefore, would best be accorded a Vindobonian or very early Pontian age. Now this is just what the radiometric datings indicate:  $\pm 12$  million years<sup>†</sup> (Leakey, in Howell & Bourlière

<sup>1</sup> The results of the extensive Harvard Expedition to Loperot, which include parts of four skeletons, will be reserved for a later paper.

1963 : 554), 14 million years (Leakey 1963 : 138 ; Evernden, Savage, Curtis & James 1964 : 174). We might therefore say that Fort Ternan has been K/A dated to the satisfaction of the mammalian palaeontologist. The rhinoceroses of Fort Ternan have not yet been described, but with this fauna are bound to be different from the Rusinga and Napak species ; their study is eagerly awaited.

The "best estimate" of a date for Rusinga,  $15.3 \pm 1.5$  million years as propounded by Evernden *et al.*, would seem to differ too little from that of Fort Ternan (12-14 million years) for such a faunal change to have taken place. A date like that of Napak ( $19 \pm 2$  million years) seems much more fitting for Rusinga, and is in keeping with palaeontological data. A fauna cannot well remain virtually unchanged for a period of several million years (if the difference in K/A dates for Napak and Rusinga amounts to that much ; both have appreciable standard errors, and the difference may be more apparent than real). One might therefore well wonder whether Rusinga has not been considered too young.

The Rhinocerotidae of Rusinga and Napak, as we have seen, would broadly correspond with the Burdigalian and Vindobonian stages in Europe. Intercontinental correlation on forms of this kind is, however, only approximate. None of the East African species is identical with any in Europe ; they probably were products of independent evolution in Africa although contemporaneous in origin with those of Eurasia. The pre-Miocene history of the rhinoceroses in Africa is sadly unknown ; none are, for example, found in the Fayum Series, at which times there had been faunal interchange between Africa and Eurasia. In Africa, rhinoceroses appear first at the Rusinga stage (unless the so-called Burdigalian fauna of Moghara, Egypt, which shows little affinity to that of Rusinga, is older).

It is feasible that *Dicerorhinus leakeyi* and *Brachypotherium heinzellini* represent more progressive evolutionary stages than the forms living at the same time in Europe (and North Africa, witness the *Brachypotherium* of Moghara), and actually are as old as the Napak K/A date indicates. Exact correlations cannot be made on the fauna so far as known. We may say that the East African Miocene fauna is approximately equivalent to the Burdigalian of Europe, but application of this Depéretian term to the East African faunal stage may easily impart a false sense of precision.

At this stage, all that can be said is that most of the Rusinga sites are tentatively accepted as correlative with the Burdigalian, the Lower Miocene of Europe, but that some sites on the island and elsewhere in East Africa appear to be younger, later Miocene or even Pliocene.

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